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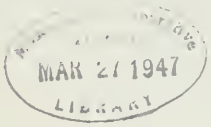

REVIEW OF THE LABYRINTHODONTIA

BY ALFRED SHERWOOD ROMER

(With forty-eight figures in the text)

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
March, 1947

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No. 1 — *Review of the Labyrinthodontia* [1]

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INTRODUCTION

The Labyrinthodontia (using the term in a broad sense) are a large and complex group of Paleozoic and Triassic tetrapods. They are of interest not alone in their own right but because of their phylogenetic position; for they appear to include, on the one hand, the basal stock of all tetrapods and, on the other, the ancestors of the reptiles and thus of all the higher vertebrate classes.

For more than a century there has been accumulating a great store of materials and data on the numerous labyrinthodont genera. However, during much of this period our knowledge of these ancient types was in general superficial in nature, and their structure — and hence their phylogeny — little understood.

A major landmark in the development of our knowledge of the group was the publication by Watson in 1919 of his important paper on "The Structure, Evolution and Origin of the Amphibia. — The 'Orders' Rachitomi and Stereospondyli". This work, supplemented by his Croonian lecture of 1925 (1926) treating of Carboniferous labyrinthodonts and amphibian origins, gave us for the first time a reasonable scheme for the morphological, and possibly for the actual phylogenetic, evolution of the group.

During the quarter century that has elapsed since this publication, great advances have been made in our knowledge of the older amphibians — advances due in no small measure to the stimulus afforded by Watson's work. In part these results have been gained by the discovery of new deposits, new forms and new material. Much, however, has been accomplished by the more thorough study of materials

both old and new, with greater attention to basic structural features significant in the interpretation of amphibian morphology, relationships and evolution.

There has been relatively little attempt in the past two decades, despite this accumulation of useful data, to review broadly the evolution and systematics of the labyrinthodonts. Such studies of this sort as have been made are discussed briefly below. Professor Watson had planned to return to this problem, but his engagement in governmental war activities has caused postponement. In the meantime my current work had made it necessary for me to review this subject as a whole. I feel that publication of the present paper will not detract from Watson's anticipated review; for although I believe that we will find ourselves in substantial agreement in many regards, there will without question be certain areas in which reasonable differences in points of view will be found and concerning which the presentation of variant viewpoints will lead, it is hoped, to profitable discussion.[1]

ORIGIN AND RELATIONSHIPS OF LABYRINTHODONTS

The base of the tetrapod stem certainly lies close to, if not within, the lower limits of the Labyrinthodontia, and the problem of labyrinthodont origins is thus essentially the problem of the origin of amphibians and of tetrapods in general. It has long been obvious that among fishes the Dipnoi and Crossopterygii present the closest approach to tetrapod — and hence labyrinthodont — ancestry, and both groups have had ardent advocates of their ancestral position. The situation was obscured by two factors: (1) the Dipnoi and Crossopterygii were believed to be only very distantly related; (2) *Polypterus* was considered to be a crossopterygian. In many features of embryology and soft anatomy the Dipnoi are demonstrably much more like amphibians than is *Polypterus*; on the other hand, the cranial anatomy of fossil crossopterygians is obviously closer to that of labyrinthodonts than the peculiar structures seen in Dipnoi, recent and fossil.

This difficulty has been resolved by the realization that Dipnoi and Crossopterygii, as increasingly demonstrated by our knowledge of fossil forms, are closely allied, and that *Polypterus* is definitely not a crossopterygian. It is thus reasonable to believe that the embryologi-

[1]As the text of this paper approached completion, I learned that Dr. E. C. Case has also prepared for publication a study of the genera of labyrinthodonts; the remarks above apply here, as well.

cal and anatomical features which lungfish and amphibians have in common were features also possessed by the early crossopterygians, and that the very different structures seen in *Polypterus* have no bearing on the case. There is therefore no bar to a belief in the crossopterygian ancestry of the labyrinthodonts and other tetrapods. Gregory, Goodrich and Watson were among the advocates of crossopterygian ancestry in the earlier decades of the present century, and recent work on that fish group has increasingly strengthened this belief. Westoll (1943) has recently given an admirable account of the structural evolution and comparisons involved and we need not enter into details here.

Säve-Söderbergh (1934 etc.) has claimed (following Wintrebert) that the tetrapods are diphyletic in origin, the urodeles having arisen, in contrast to all other tetrapods, from forms allied to the dipnoans, and has proposed a classification to express this viewpoint. Various features of the urodeles suggest that they may have diverged at a rather early stage of tetrapod evolution from lines leading to frogs and to amniotes (cf. the discussion, below, of vertebral types). But these differences are so far outweighed by the great array of characters which they possess in common with other tetrapods, that this theory cannot be seriously entertained unless substantial evidence is presented for it — which is not the case.

Although reserving detailed discussion for later sections, the general nature of the groups here included in the Labyrinthodontia may be noted.

It is the writer's belief that the Amphibia may be divided into two major groups, and that the structure of the vertebral centra forms an effective key to this dichotomy. In typical Labyrinthodontia, as in crossopterygians on the one hand and early reptiles on the other, the centra appear to have ossified from cartilaginous blocks as centers, these blocks appearing as intercentral and pleurocentral structures of various sorts and corresponding in general (although often not in detail) with the arcualia of Gadow's concepts. I have suggested that amphibians with this type of vertebral structure be considered as forming a Subclass Apsidospondyli, the name referring to this feature. Here are to be included the Labyrinthodontia and the Anura. The latter, on current evidence (Watson 1940), are apparently members of this group in which the ventral arcualia have been reduced.

Quite in contrast are the modern Urodela and Apoda, in which there are no typical cartilaginous blocks representing the centra, and the formation of vertebral centra takes place by direct ossification

around the notochordal tube. Although embryological confirmation is, of course, lacking, a similar type of central construction appears to have been present in a variety of Paleozoic amphibians to which such terms as Nectridia, Aistopoda, Microsauria and Adelospondyli have been applied. Many or all of these Paleozoic groups are frequently referred to collectively as the Lepospondyli (Zittel); this appropriate term ("husk vertebrae") may well be expanded and used as a subclass term embracing the Urodela and Apoda as well as the antecedent extinct groups.

Lepospondyli and Apsidospondyli presumably diverged at an early stage, for lepospondyls are known from very low levels in the Scottish Mississippian series. However, despite the differences in vertebral construction, and certain other features as well, the non-piscine resemblances between early lepospondyls and early labyrinthodonts are so numerous that it is reasonable to deduce that their common ancestor had attained an amphibian level of organization. Since the structure of the labyrinthodonts appears to approximate crossopterygian structure more closely than that of even the most primitive known lepospondyls, it is reasonable to believe that the lepospondyl ancestors were primitive labyrinthodonts. It is, however, possible that the lepospondylous condition has arisen more than once, and that the Lepospondyli are polyphyletic in origin.

HISTORY OF CLASSIFICATION

In early years of the present century the labyrinthodonts (or the greater part of them, at least) were generally termed the Temnospondyli (Zittel) and usually considered to be a suborder of the "Stegocephalia", the latter blanket term including all of the pre-Jurassic amphibians of any kind. The forms with rhachitomous and embolomerous vertebrae were almost universally included in the temnospondyls, the stereospondyls sometimes included, sometimes placed in a separate suborder. The little branchiosaurs were, as a supposedly discrete group, considered to form a separate suborder, the Branchiosauria or Phyllospondyli (Credner); *Seymouria*, here classed with the labyrinthodonts, was considered a cotylosaur and hence a primitive reptile, and some types which we now know to be labyrinthodonts were included in Dawson's group Microsauria, or included among the lepospondyls, or left *incertae sedis*.

Perhaps typical of these earlier classifications is that in Eastman's translation and edition of Zittel's "Grundzüge" (1902):

Order Stegocephalia
Suborder Phyllospondyli. Family Branchiosauridae
Suborder Lepospondyli (including a few labyrinthodonts)
Suborder Temnospondyli (not divided into families; various rhachitomes and embolomeres)
Suborder Stereospondyli. Family Gastrolepidotidae (including a few embolomeres). Family Labyrinthodontidae (various stereospondyls).

A new era in the history of the study of amphibian evolution and classification was initiated as noted above with the publication in 1919 of Watson's first major contribution to the subject. He revived the use of Owen's term Labyrinthodontia for the group under consideration, and demonstrated a series of structural stages through which the labyrinthodonts had evolved in successive geological periods — Carboniferous, Permian, Triassic. In the Carboniferous many, at least, of the primitive types possessed embolomerous vertebrae; in the Permian, rhachitomous forms dominate; in the Triassic, stereospondylous genera. Using vertebral structure as a nomenclatorial basis, three "grades" were established to include the members of successive structural stages. It will be noted that Watson in his use of terms carefully avoided any implication that successive structural stages were reached in monophyletic fashion and, in fact, emphasized the probability that a great deal of parallel evolution had occurred. In Watson's scheme, the branchiosaurs are treated as a separate group, and he long considered *Seymouria* as a reptile (1919a; cf. 1942).

Watson's classification, developed in publications of 1919, 1926, 1929 and 1940, is as follows:

Order Labyrinthodontia
Grade Embolomeri
Superfamily Anthracosauroideae. Families: Eogyrinidae, Palaeogyrinidae, Otocratidae, Cricotidae
Superfamily Loxommoideae. Family Loxommidae
Grade Rhachitomi. Families: Eryopidae, Actinodontidae, Rhinesuchidae, Achelomidae, Dissorophidae, Trematopsidae, Zatrachydae, Archegosauridae, Trimerorhachidae, Lydekkerinidae, Micropholidae, Dwinasauridae.
Grade Stereospondyli. Families: Capitosauridae, Trematosauridae, Metoposauridae, Mastodonsauridae, Brachyopidae.
Order Phyllospondyli. Families: Eugyrinidae, Branchiosauridae, Melanerpetonidae, Miobatrachidae.

Abel in 1919 classified the labyrinthodonts as follows:

Subclass Stegocephalia

Order Rhachitomi = Temnospondyli. Families: Archegosauridae, Trimerorhachidae, Eryopidae, Trematopsidae, Dissorophidae, Aspidosauridae, Zatrachydae, Micropholidae, Labyrinthodontidae, Plagiosauridae.

Order Embolomeri. Family Cricotidae.

Order Phyllospondyli. Families: Branchiosauridae, Acanthostomidae.

The "Family Labyrinthodontidae" includes nearly all the Triassic genera as well as some Carboniferous genera now known to be embolomeres.

A notable feature in Abel's classification, essentially followed in Säve-Söderbergh's scheme and in that here proposed, is the sharp separation of the embolomeres (as far as then identified) from the remaining types for which (including the stereospondyls) are used the terms Rhachitomi (in a broad sense) or Temnospondyli (in a somewhat restricted sense).

Huene in 1920 proposed an arrangement of the Triassic families similar to that of Watson's (with which he was not as yet acquainted). In 1931 (1931a) he gave a complete classification in which he followed Watson in most points:

Labyrinthodontia.

Embolomeri.

Superfamily Anthracosauridae. Families: Eogyrinidae, Palaeogyrinidae, Otocratidae, Cricotidae.

Superfamily Loxommoideae. Family: Loxommidae.

Rhachitomi. Families: Eryopidae, Actinodontidae, Archegosauridae, Rhinesuchidae, Achelomidae, Dissorophidae, Lydekkerinidae, Micropholidae, Dendrerpetontidae, Melosauridae, Zatrachydidae, Trimerorhachidae, Platyopodidae, Dwinasauridae.

Stereospondyli. Families: Trematosauridae, Mastodonsauridae, Capitosauridae, Metoposauridae, Rhytidosteidae, Brachyopidae.

Pseudocentromorpha. Including:

Superfamily Branchiosauridae. Families: Colosteidae, Peliontidae, Stegopidae, Branchiosauridae.

Smith Woodward, in his 1932 revision of the Zittel-Eastman text, tended, as he notes, to be conservative in classification, but was

obviously strongly influenced by Watson's work. His treatment is as follows:

Suborder Temnospondyli

A. Embolomeri. Families: Anthracosauridae, Loxommidae, Pholidogasteridae, Cricotidae, Seymouriidae

B. Rhachitomi. Families: Archegosauridae, Eryopidae, Rhinesuchidae, Zatrachysidae, Trimerorhachidae, Lydekkerinidae, Micropholidae, Cochleosauridae, Dvinosauridae, Trematopsidae, Dissorophidae.

C. Stereospondyli. Families: Trematosauridae, Capitosauridae, Metoposauridae, Mastodonsauridae, Rhytidosteidae, Brachyopidae.

Suborder Phyllospondyli. Family Branchiosauridae.

As noted in a later section, the concept of the Phyllospondyli as an independent group of small Paleozoic amphibians underwent considerable expansion during the period under discussion. Originally confined to the branchiosaurs, this supposed group grew, in the hands of Watson, Steen and the writer, to embrace a great variety of Carboniferous amphibians. These now appear, however, to be actually labyrinthodonts of various sorts, mainly of small size and frequently immature (Romer 1939a).

In a fine series of papers descriptive of Permian and early Triassic amphibians from the Ural region, Bystrow and Efremov have developed the valuable and useful concept of a neorhachitomous stage in labyrinthodont evolution. They have not, however, attempted any general reclassification of the labyrinthodonts as a result of their work, although calling attention to various phylogenetic points.

Säve-Söderbergh in 1934 proposed a scheme of classification of the vertebrates which in many regards widely departs from any other previously suggested. The classification of the area with which we are here concerned was elaborated in a paper of 1935 in which the literature of skull patterns of labyrinthodonts was reviewed:

Superorder Batrachomorpha
  Order Ichthyostegalia
  Order Labyrinthodontia
    Suborder Loxommoidei
    Suborder Capitosauroidei
      Superfamily: Eryopoideae. Families: Eryopidae, Zatrachydidae, Rhinesuchidae, ?Acanthostomatidae, ?Achelomidae, ?Melosauridae, ?Trematopsidae.

Superfamily Capitosauroideae. Families: Wetlugasauridae, Capitosauridae, Mastodonsauridae.
Suborder Trematosauroidei
Superfamily Metoposauroideae. Families: Trimerorhachidae, ?Dissorophidae, Metoposauridae.
Superfamily Trematosauroideae. Families: Trematosauridae, Peltostegidae, ?Archegosauridae.
Suborder Brachyopoidei. Families: Dvinosauridae, Brachyopidae.
Labyrinthodontia incertae sedis: Actinodontidae, Lydekkerinidae, Rhytidosteidae.
Order Phyllospondyli
Also includes ?Order Anura
Superorder Reptiliomorpha
Order Anthracosauria
Order Seymouriamorpha
Also includes Reptilia, Aves, Mammalia — apparently as "orders"!

This scheme rests almost entirely upon a few points concerning dermal skull roof proportions and patterns, and is hence, as Bystrow and Efremov (1940, p. 142) note, based on very superficial data. Nevertheless, a major change in classification which he makes on a consistent although a minor feature — the size and relationships of the tabular[1] — is justified by a broader consideration of the situation. It is increasingly apparent, as our knowledge of early amphibians increases, that while Watson's conception of a primitive level of structural organization characteristic of Carboniferous labyrinthodonts is a valid one, the primitive types are not all embolomeres. The Embolomeri proper are a more restricted group, allied to the seymouriamorphs and early reptiles; the loxommids, included by Watson among the embolomeres, are more probably affiliated with the Rhachitomi.

The term Labyrinthodontia is by Säve-Söderbergh limited in general to the forms customarily grouped as the Rhachitomi and Stereospondyli. His classification of this group at first sight bears the appearance of a radical difference from older ones; the various families are arrayed in unfamiliar groups. On closer examination, however, a familiar pattern reappears. His Superfamily Eryopoideae is essentially the Rhachitomi with a few families subtracted; the groups which follow are essentially the former Stereospondyli divided into major components. This arrangement is a bold attempt to carry

[1]Säve-Söderbergh's discussion of this point is obscured by his unusual nomenclature and philosophy of evolution of dermal elements (cf. the discussion in a later section), but has been clarified by Steen (1938, p. 276 ff.).

to a logical conclusion the implications of polyphyletic derivation of the stereospondyls which are contained in Watson's work. I believe that certain features of this arrangement are justified after a full consideration of the evidence; but the treatment of the matter here is superficial indeed. Elaborate definitions are given of the various groups; but if these are analyzed, it will be seen they are almost entirely associated with three simple features: length of skull; rounded or pointed snout; position of the orbits. A classification on such bases amounts to little more than a sorting out of skull types very similar to that noted by Watson (1919, p. 50). But as Watson rightly points out, these features are highly adaptive in nature and form no grounds in themselves for a classification. Säve-Söderbergh's association of metoposaurs and trematosaurs in a single suborder is exceedingly incongruous. Various categories include with Triassic families presumed Permian ancestors with supposedly similar skull contours. Some of these associations are quite possibly of merit. But, on the other hand, the association of the dissorophid *Broiliellus* in a common group with *Trimerorhachis* and the metoposaurs makes strange bedfellows.

Kuhn in a valuable summary of our knowledge of fossil amphibia published in 1939 (1939b), gives the following scheme:

Order Labyrinthodontia
- Suborder Embolomeri
  - Superfamily Anthracosauroidea. Families: Eogyrinidae, Palaeogyrinidae, Otocratiidae, Cricotidae.
  - Superfamily Loxommoidea. Family Loxommidae.
- Suborder Rhachitomi. Families: Dendrerpetontidae, Eryopsidae, Rhinesuchidae, Dissorophidae, Trematopsidae, ?Zatrachydidae, Archegosauridae, Trimerorhachidae, Lydekkerinidae, Micropholidae, Cochleosauridae, Dvinosauridae.
- Suborder Stereospondyli. Families: Trematosauridae, Mastodonsauridae, Capitosauridae, Metoposauridae, Brachyopidae (Plagiosauridae).

Order Phyllospondyli. Families: Ichthyostegidae (?), Colosteidae, Peliontidae, Branchiosauridae, Stegopidae (including Zatrachydidae?), Melanerpetontidae.

This classification (cf. Romer 1940) in general follows that of Watson and, as regards the phyllospondyls, follows Steen and the writer in our distention of that group to bloated proportions.

The writer's scheme of classification is developed in the course of the systematic discussion of genera and higher groups in the later part of this paper and is presented in a concluding section. Although anticipating later discussion, we may here note the general nature of the classification arrived at and the array of forms included.

Comprising the Labyrinthodontia (in the form of a superorder) are all types usually placed in that category. Also included are the Ichthyostegalia, the Seymouriamorpha, the "Phyllospondyli", and certain genera sometimes placed in the lepospondyl groups because of inadequate data or inadequate consideration.

A primary cleavage into two groups appears to be indicated. One group includes the rhachitomes and stereospondyls and also, apparently, the loxommids and ichthyostegids. This large assemblage I shall term the Temnospondyli. Säve-Söderbergh has used Labyrinthodontia in a restricted sense for this group, but it seems preferable to retain this latter term in its current broader sense. The term Temnospondyli was at one time generally used for rhachitomes and stereospondyls with little thought of the embolomeres (or seymouriamorphs); some writers (e.g. Abel 1919) have definitely excluded the embolomeres from the Temnospondyli and used the term in essentially the present sense. Within the Order Temnospondyli I have included, as suborders, the Ichthyostegalia, Rhachitomi, Stereospondyli and Trematosauria. Rhachitomi and Stereospondyli are somewhat modified in content; the trematosaurs, usually included in the latter, are here given separate status.

For the more reptile-like forms, an emendation of previous usages of Watson, Säve-Söderbergh and Steen makes the Anthracosauria available in an ordinal sense. Included here are the embolomeres (less the loxommids) and the *Seymouria* group, representing the closest approximation to the reptiles.

As demonstrated most clearly by Watson, the later labyrinthodonts followed, apparently in various parallel phyletic lines, an evolutionary trend toward a flattened body and skull, a lower degree of ossification of the skeleton and braincase and toward the development of other features which from many points of view one inclines to characterize as regressive or degenerate. Many of the features seen, however, are apparently adaptive in nature. We shall here refer to forms in this category as "advanced", with the understanding that this term implies merely that they have progressed far along this evolutionary pattern, without philosophical implications as to the direction — upward or downward — of the progress made.

Although we shall discuss various points of taxonomy, the present paper is not intended as a formal systematic revision, and no attempt is made to give full references to taxonomic variations. References, although comprehensive, are, rather, to the more important morphological and stratigraphic works.

Apart from a number of comparative morphological figures, our illustrations are almost entirely confined to a series of dorsal and ventral skull views of such genera as are well enough known to render such illustration possible. Although certain of these figures are in whole or in part original, most are derived from the various sources acknowledged. In order to give as complete a series as possible, I have freely made composites of separate figures and restored and simplified various features in order to facilitate comparative study. It must, therefore, be emphasized that these figures are in no way to be regarded as primary sources.[1]

At one time or another I have studied the materials of the greater part of the forms concerned in the various museums of the United States, western and central Europe and South Africa. There are, however, notable collections which I have not seen, particularly recently gathered materials of Triassic amphibians in Russia and Scandinavia; and even in the case of the material studied by me, I have relied in very considerable measure upon the published work of others rather than upon my own observations, often of necessity hasty and superficial.

Miss Nelda Wright aided throughout the preparation of the manuscript and prepared the illustrations. I am further grateful to Dr. Tilly Edinger for a critical reading of the manuscript.

GENERAL MORPHOLOGY

Despite our great advances in knowledge of individual types there has been no recent general account of labyrinthodont morphology. I shall here attempt this as a framework upon which to base the morphological discussion, in the following sections, of the various groups and genera concerned.

SKULL-SURFACE TOPOGRAPHY

The central type of labyrinthodont skull, as regards general shape, is that seen in a great variety of forms such as (for example) *Ichthyostega, Eryops, Capitosaurus* and *Palaeogyrinus*. The skull is broadly

[1]For page references to figures and explanation of abbreviations see p. 368.

rounded anteriorly, and increases somewhat in breadth toward the back, most of the expansion occurring posterior to the orbits. The quadrate region in primitive forms is generally situated well posterior to the level of the occiput; as Watson has noted, there is a strong tendency, associated with feeding habits, toward shortening the suspensorial region in late flat-headed forms. The orbit is typically situated somewhat back of the mid-length of the skull, but there are numerous variations; either primitively or secondarily the orbits may be placed relatively far forward (as in *Erpetosaurus, Trimerorhachis,* metoposaurs); conversely the skull table posterior to the orbits may be relatively short. A long and relatively slender snout is developed in many cases, such as certain embolomeres, *Archegosaurus,* and trematosaurids, seemingly in association with piscivorous habits. Notably in Triassic forms, the skull may be excessively shortened, giving a parabolic skull outline.

As noted particularly by Bystrow (1935), the skull in larval stages is short, especially in the antorbital region, and the suspensorial region relatively far forward; retention of such conditions in the adult may be due to neoteny. As that author notes, the sculpture pattern of the dermal roofing elements gives evidence in this respect. Säve-Söderbergh has commented on the zonal nature of post-embryonic growth in the dermal roof.

The posterior margin of the skull is interrupted on either side by the otic notch, presumably containing the ear-drum and derived from the spiracular notch of the crossopterygian skull. The notch is of variable construction; in embolomeres it is a V-shaped cleft with a loose attachment of cheek and skull roof anterior to it; in most other forms it is more rounded, with the cheek and roof elements firmly fused along its anterior border. The degree of notch development is quite variable. In some, its size is exaggerated; in others it may be eliminated in great measure, giving a nearly straight contour to the posterior margin of the skull. The notch may be partially or completely enclosed, posteriorly, in various ways as seen in *Otocratia,* aspidosaurs, *Trematops, Cyclotosaurus.*

Almost without exception a parietal (pineal) opening, sometimes of considerable size, is present between the parietals. The paired orbits are usually far removed from the mid-line. They are of variable size, a feature partially (but not exclusively) correlated with the absolute size of the form concerned. Their contours are usually circular, but in some cases (notably loxommids) additional areas, obviously not concerned with the eyeball, are included and have been

suggested as the loci of glandular developments. In primitive types the planes of the orbits faced laterally as well as dorsally; in flat-headed forms, presumably bottom-dwellers in many cases, they faced dorsally. The orbital margins may be elevated, notably the medial border.

The external nares are characteristically subcircular openings of modest size. Exceptionally (as in *Trematops*) they may be enlarged, presumably for glandular structures, and in a few cases a small median rostral opening, also presumably for a gland, is reported. In most cases the external naris is, although lateral in position, separated from the skull margin by a broad firm union of maxilla and premaxilla. In certain early and seemingly primitive types, however, the naris is close to the margin and the union of the elements lateral to it relatively weak or even (ichthyostegids) absent. In temnospondyls the external nares are generally placed well back from the tip of the snout and well toward the lateral margin of the skull; in anthracosaurs they are situated more anteriorly and medially.

As seen in lateral view, the skull was moderately high in primitive forms, as was the case in the presumed fish ancestors. This height appears to have been retained in many embolomeres and seymouriamorphans (as in the related reptiles). In most cases, however, the skull becomes progressively flattened, presumably in association with the development of sedentary bottom-dwelling habits.

The region anterior to the orbits is typically evenly rounded in cross-section. Posteriorly a line from orbit to otic notch separates a flattened median dorsal region, the skull table, from the more vertically placed cheek region on either side.

DERMAL SKULL ROOF

The dermal elements of the skull roof (and those of the outer surface of the jaw as well) bear a rugose sculpture which presumably was tightly bound to the overlying skin and is comparable to that found today on the crocodilian skull. Most characteristically, this sculpture takes the form of a series of anastomosing ridges, between which are short valleys or pits; the pattern of sculpture radiates from the centers of ossification of the elements concerned. In some cases the ridges are prominent in the picture, the depressions open valleys; in others, the general effect is that of a pitted surface.

A system of grooves carrying lateral line organs is frequently present on the surface of the roof elements; the presence of these

grooves is reasonably to be correlated with purely aquatic habits. In bony fishes the lateral line organs are typically enclosed in canals sunken beneath the bone surface. This structure is found in amphibians only in a few cases.

The morphology and nomenclature of these grooves has been discussed by Säve-Söderbergh (1933) and Westoll (1943, pp. 87, 89), among others. Typically a groove runs forward over the lateral margin of the skull table as an anterior continuation of the main lateral line of the body, usually traversing the tabular and the temporal elements. It then turns downward, as a suborbital groove, over the postorbital and jugal to run forward below the orbit to the narial region along the maxilla, usually with a short diversion, sometimes in the form of a Z, onto the lacrimal. Frequently joining this is a second major groove, the supraorbital, running forward above the orbit. From their shape the supraorbital grooves are frequently termed the lyrae. In most cases the supraorbital traverses postfrontal, frontal, prefrontal, lacrimal and nasal along its course to the premaxilla. A groove typically passes back in the cheek region from the jugal over the squamosal and, curving ventrally over the quadratojugal, appears to have been continuous in life with a groove along the outer surface of the lower jaw. In addition to the system of major grooves, minor ones are occasionally present which Westoll compares to the pit-lines of fishes, accessory to the major lateral line organs. In fishes the lateral line canals appear to be intimately associated ontogenetically and phylogenetically with specific dermal elements; there is relatively little evidence of intimate association between the comparatively superficial amphibian grooves and the underlying bones.

A major series of bones of the skull roof are paired elements lying along the longitudinal axis. These include, from front to back, the nasals, frontals, parietals and postparietals.

The nasals are usually rather broad elements, lying adjacent to the premaxillae anteriorly and the frontals posteriorly. Laterally they are usually in contact with both prefrontals and lacrimals, and with the septomaxilla when that element is exposed on the surface. There was little or no contact with the lacrimal in the ichthyostegals, little contact with the prefrontal in embolomeres. With reduction of the lacrimal in advanced rhachitomes and stereospondyls, nasal and maxilla meet posterior to the external naris.

The frontals are typically large and somewhat rectangular elements, lying between nasals and parietals, centered rather in advance of the orbits. In certain forms, particularly some stereospondyls, in

which the eyes are rather close together, the frontals may form part of the orbital margins; usually they are excluded from the orbit, and prefrontal and postfrontal form the entire lateral boundary of the frontals.

The parietals occupy a prominent central position on the skull table, with their growth centers close to the parietal foramen, well back of the level of the orbit. Postfrontal, intertemporal (when present) and supratemporal usually bound the parietal laterally. In ichthyostegals the postorbital is in contact with the parietal; in anthracosaurs the tabular meets the parietal at its postero-lateral corner. Most or all of the posterior margin of the parietal is bordered by the postparietal.

The postparietal (interparietal, dermal supraoccipital) is in most forms an element of rectangular shape which forms much of the posterior margin of the skull table posterior to the parietal. It is usually definitely a paired structure. It is of large size in ichthyostegals suggestive of a transitional condition from the crossopterygian stage, in which it occupies a considerable proportion of the skull length. In most cases it is bounded anterolaterally by the supratemporal, laterally by the tabular; in anthracosaurs the former contact is absent. The postparietal is in contact on its under surface with the supraoccipital region of the braincase, and may send downward an occipital flange, sheathing much of that region.

In various instances accessory median elements (studied particularly by Broili, 1917, etc.) may be present in the skull roof. Early ichthyostegals have a median internasal element between premaxillae and nasals, perhaps a hold-over from a crossopterygian condition, and some loxommids appear to show a similar structure; *Eryops* has a characteristic interfrontal, etc.

The premaxilla and maxilla are distinctive in that they bear the marginal tooth row. The dorsal exposure of the premaxilla occupies the region of the snout anterior to the nasal bone and the external naris. In general there is a firm union with the maxilla lateral to the external naris; in ichthyostegals and loxommids this union is weak or absent — presumably a primitive condition. The extent of development of the maxilla along the margin of the cheek appears to be correlated closely with the length of the tooth row. Its tapering posterior tip in some cases reaches the quadratojugal but in most forms the maxilla terminates more anteriorly — frequently at a point about two-thirds back along the length of the skull. In general the lacrimal and jugal form most or all of its median boundary.

Anteriorly it forms part of the narial border and just back of that opening may be in contact with the septomaxilla or, when the lacrimal is reduced, may meet the nasal. Only very exceptionally does the maxilla reach the orbital border. There is seldom any tendency for the maxilla to reach the depth in the preorbital region that it gains in many reptiles.

Frequently grouped as a circumorbital series are five bones — prefrontal, postfrontal, postorbital, jugal, lacrimal. The prefrontal forms part of the dorsal and anterior borders of the orbit and typically extends a considerable distance forward along the upper part of the facial region, lateral to the frontal; in most cases there is a broad contact, still farther forward, with the nasal. In primitive types the lacrimal forms the entire lateral boundary of the bone; when the lacrimal is reduced, prefrontal and jugal may meet along the orbital boundary. In short-faced forms the pointed anterior tip of the prefrontal may approach closely the narial opening (and reaches the expanded opening of trematopsids), and may, exceptionally, but perhaps primitively, touch the septomaxilla.

The postfrontal is a posterior analogue of the prefrontal, typically forming the postero-medial margin of the orbit and generally extending backward between the postorbital laterally and frontal and parietal medially to meet the supratemporal or the intertemporal, if the latter is present. Except in a few forms, pre- and postfrontals are in contact above the orbit.

The postorbital normally occupies a considerable area along the posterior margin of the orbit between postfrontal above and jugal below. The postero-lateral margin is formed by the squamosal; the supratemporal and intertemporal (when present) form part of the median boundary, and the bone usually terminates posteriorly as a wedge between the first two of these elements. An exceptional condition is found in the ichthyostegals, where it meets the parietal broadly and tends in later members of that group to be partially or completely excluded from the orbital margin.

The jugal is generally an elongate element of the cheek, lying medial to the maxilla for much of its extent and forming the ventral margin of the orbit. In many forms it reaches the lateral margin of the skull between maxilla and quadratojugal. There is typically a short suture between the jugal and the last named element posteriorly; the upper boundary in the cheek region is formed by postorbital and squamosal. The width of the jugal beneath the orbit is variable, depending upon the relative size of that opening. Very variable is

the anterior development of the jugal. In forms in which the lacrimal is reduced and recedes from the orbital rim, the jugal extends upward in this area to the prefrontal and may have a considerable expansion on the face between maxilla and lacrimal.

In a relatively few forms, seemingly primitive or reptile-like, the lacrimal extends, as in early reptiles, the full distance from orbit to naris (or to the septomaxilla when that bone is developed externally). In most cases, however, the lacrimal fails to reach one extreme or the other — or both. It is bounded medially by nasal and prefrontal, laterally by the maxilla, and the jugal is variably present in its lateral or posterior margins. There is seldom evidence of the presence or absence of a lacrimal duct, but it appears to have been generally absent.

For want of a better place, the septomaxilla may be mentioned here — a small dermal element, sometimes exposed superficially at the posterior or medial margin of the external naris, sometimes situated within the narial cavity — and usually, it would appear, destroyed in preparation when present.

Behind the postfrontal, we find a row of elements occupying the temporal region. They form the lateral margin of the skull table and are bordered medially by parietal and postparietal, laterally by postorbital, squamosal and the otic notch. These elements include intertemporal, supratemporal and tabular. The first is variable in occurrence, and the others vary in size and relative position, but the total area of the three combined is in general a constant.

The intertemporal is present in anthracosaurs and a number of rhachitomes, mostly primitive in nature; it is absent in other groups, including ichthyostegals, advanced rhachitomes, trematosaurs and stereospondyls. It occupies an area which in its absence is generally covered in variable fashion by the postfrontal and supratemporal or, in ichthyostegals, by postorbital and parietal. When present it is bounded by the four elements just mentioned.

Next posteriorly is the supratemporal, lying essentially between parietal and squamosal and forming part of the medial margin of the otic notch when that structure is well developed. Except in ichthyostegals the bone is in contact anteriorly with the postfrontal or the intertemporal if present; antero-laterally there is a postorbital contact; posteriorly one with the tabular. In temnospondyls there is a rather long suture with the postparietal; in anthracosaurs, where the tabular is relatively well developed and the postparietal small, this last contact — a useful diagnostic feature — is lost.

The tabular forms the postero-lateral margin of the skull table. Primitively it was bounded laterally by the otic notch, but when the notch is reduced in size (ichthyostegals, some stereospondyls, etc.), a sutural connection is gained with the squamosal. The tabular braces the paroccipital process and may be greatly thickened ventrally in this area, as well as sending down an occipital flange.

The main element of the cheek region is the squamosal, filling out most of the expanse of this region between the temporal elements above, the postorbital anteriorly, the jugal and quadratojugal below, and the quadrate and the margin of the cheek posteriorly. Along this last margin the squamosal curves over inwardly to gain, in most instances, a broad union with the pterygoid, and may even gain contact by a descending process with the epipterygoid as well (details are known in but few forms). As noted previously the dorsal relations of the squamosal are variable; in embolomeres a loose union with the supratemporal in advance of the otic notch, in other groups a stout sutural union with supratemporal and, with notch reduction, a similar stout union with the tabular.

A minor cheek element is the quadratojugal. This fills in the far corner of the cheek region, beyond the reach of jugal and squamosal; it usually enters into intimate relations with the quadrate and may form part of the region for the jaw articulation. In the ichthyostegids a preopercular bone persists in this region as a hold-over from the fish condition.

CONCEPTS OF DERMAL ROOF EVOLUTION

The skull roof pattern of dermal bones figures conspicuously in discussions of amphibian phylogeny and classification, since this area of the skull is the region most frequently preserved and described, and since the varying arrangement of the elements lends itself readily to the formation of simple diagnoses. It is well, however, to consider the general history and nature of the dermal roof elements in order that a proper perspective may be gained as to the degree to which reliance may be placed on these structures as clues to amphibian relationships.

In the study of roofing bones one tends to think of the various elements as discrete, independent structures. Historically, however, we can see that this development of "individuality" of the elements is a relatively late phenomenon in vertebrate evolution, and that the early history was one in which the parts were markedly subordinate

to the whole — the skull roof a structural and functional unit forming an effective dorsal shield to the head structures. As suggested by conditions in Paleozoic (particularly Devonian) bony fishes (cf. Romer 1936, pp. 255–256) this shield was, it seems, a solid structure in which sutures between bony elements were, in the adult, little in evidence and frequently obliterated. The individual elements were merely convenient centers for the initiation in the embryo of ossifications which were to be fused into a unit in the mature roof. Retention of the sutural lines between elements instead of complete fusion was essentially a "convenient" method of permitting further growth and expansion in size of the shield.

The evidence from early fishes indicates the probability that initially the ossification centers in the shield were numerous and variable; the exact means by which the ossification was accomplished made little difference as long as the end result — the ontogenetic development of a complete and solid shield — was accomplished (cf. Westoll 1943). In the evolution of various fish groups — and the amphibians as well — it would appear that there was a gradual reduction in the number of centers employed and a tendency for the development of a comparatively stable pattern composed of a relatively small number of elements. There is little likelihood, *a priori*, that the surviving centers would be precisely the same in any two major groups, and hence the determination of homologues between the skull elements of the various fish assemblages presents great if not insuperable difficulties.

Tetrapod skull elements, on the other hand, may vary in area occupied, become reduced and lost, or fuse by the elimination of sutures in late ontogenetic stages; but their identity can in general be readily followed throughout. It is a generally accepted principle that in the nomenclature of vertebrate structures mammalian names be used wherever possible. Because of the stability of tetrapod skull elements, we are able to apply mammalian names with confidence to many of the roofing bones in amphibians, and considerable agreement has long since been reached on the nomenclature of elements lost in mammals. The nomenclature was well standardized by the time of the publication of the committee report on this subject in 1917 (Gregory 1917) and the names there adopted are those used, with few variations, by almost all workers.

Within the tetrapods, the roof pattern has attained a stable state. From amphibians through reptiles to birds and mammals, there is almost never any addition of new elements. There are, however,

losses of elements in more progressive (or degenerate forms). In most cases it is evident that a situation under which the area formerly held by an absent element is occupied by one or more of its neighbors can be attributed to gradual reduction and final loss of the ossification center concerned, rather than to any "fusion" of one center with another. Fusion of elements may occur (the adult bird skull is an outstanding example); but such fusion is almost always demonstrably a phenomenon of late ontogenetic development; in the embryo, where known, the ossification centers remain distinct. Again, the area occupied by an ossification center may vary greatly; but the elements concerned are usually readily identified, despite the variations.

In Säve-Söderbergh's papers discussing amphibian skull roof patterns he has used a terminology radically different from that in general use. This practice appears to be in great measure due to his lack of understanding of the history and methods of work in the field of tetrapod morphology, and will, one may trust, be speedily abandoned because of the confusion it creates. Worthy of discussion, however, is his acceptance — as revealed by his frequent use of compound names — of concepts of the nature and history of dermal roof elements quite different from that outlined above. These concepts have been widely used in studies on fishes — particularly the actinopterygians, recent and fossil.

In the early history of the study of the fish skull it was obvious that the homology of the fish dermal bones with mammalian skull elements was impossible to determine accurately, and mammalian names were applied to fish elements in a frankly arbitrary fashion. Further complications, however, were present. The number and arrangement of bones varied widely within the actinopterygians; in one form, for example, two or three bones may be present in the area where but a single element is found in a second type. From this sort of situation rose the concept that the primitive fish skull roof was composed of a large number of elements of small size, each intimately associated with some specific area or feature of the skull roof; and that the variations in arrangement in known forms were due to the fusion in variable fashion of these theoretical "aboriginal" elements into larger and complex ones. The terminology of these elements was effected by compounding the names assigned to their hypothetical components.

That the fish dermal roof originally consisted of numerous small elements is a belief on which general agreement can probably be reached. That, however, these original elements were stable and

closely associated with definitely bounded areas is unproved and is highly unlikely on current evidence. There is little to show that many of the fish elements to which compound names are given, are in any way the result of any sort of "fusion", real or theoretical, and they may be more reasonably interpreted as having the type of history definitely seen in many tetrapod cases, i.e., a "survival of the fittest", elimination of small elements and occupancy of their territory by their neighbors.

When this type of theoretical treatment applied to fishes is carried over into the Amphibia, it leads to unnecessarily complex interpretation of relatively simple matters. The case of tabular variation is a case in point. This interesting detail of skull roof pattern was first clearly identified by Säve-Söderbergh as a useful clue to a major subdivision of the labyrinthodonts. As may be seen from an inspection of skull roof series, there are two distinct patterns in the tabular area. In one, characteristic of the great majority of labyrinthodonts, the tabular is small and does not meet the parietal, and in consequence supratemporal and postparietal are in contact; in the other, seen in the anthracosaurs, the reverse situation holds, and the tabular and parietal have a common suture.

This variation is interpreted by Säve-Söderbergh (1935, fig. 45 etc.) in elaborate fashion. He assumes that in addition to the four known elements in this region, there is an extra element between postparietal and tabular which sometimes fuses with the one element, sometimes with the other (Fig. 1, A), and that the parietal is a compound, of which a posterior component may sometimes remain with the rest of the parietal, sometimes fuse with the postparietal.

This seems to be an unnecessarily round-about way of accounting for a simple variation, and one's scepticism is aroused by the fact that the extra elements introduced into the picture are quite unknown as independent structures.

The basal difficulty which has apparently necessitated the development of this elaborate theoretical interpretation seems to be the concept that the boundaries between elements are fixed lines that cannot be transgressed. As the later history of tetrapods demonstrates, this concept has little if any validity. Ontogenetically, ossification in a membrane bone spreads outward from its center without (so to speak) any knowledge of hypothetical boundaries which it is not supposed to transgress. When the spreading ossification meets that from another center, expansion ceases and a sutural line is established between the two elements. Variations in position of the line of suture

may be caused by differences in the time of establishment of the centers concerned, in their relative position, and in the rate of growth. The situation is analogous to the deployment of two opposing armies; a line of battle (i.e., a suture) tends to be established midway along a line connecting the two headquarters and at right angles to this line, but the position of the line of battle may vary according to the point of concentration of the opposing armies, the speed of mobilization and deployment, etc.

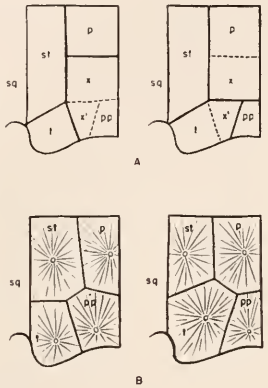

Fig. 1. *A*, diagrams of the dermal elements of the left half of a labyrinthodont skull table, to show variations in the relations of the tabular and adjacent elements according to the theory of Säve-Söderbergh. *Left*, the temnospondyl type. The tabular is small, and fusion of hypothetical elements x, x' with postparietal give that bone contact with the supratemporal and cut tabular off from parietal. *Right*, anthracosaur condition; x has fused with parietal, x' with tabular, so that these elements are in contact, and postparietal is separated from supratemporal. *B*, diagrams to illustrate the explanation advocated in the text. Variation in contacts can be explained by differences in position of ossification centers and in rate of growth from those centers, without the necessity of calling upon additional hypothetical elements.

On this view, based on the facts of ontogeny, variations in size of the tabular and related elements may be accounted for very simply in terms of variation in position of ossification centers, in the time of their establishment, or the rate of growth from them. Even if we confine ourselves to the first of these factors alone, it can be readily demonstrated (Fig. 1, B) that a rather small change in the position of the centers concerned will result in a striking difference in sutural pattern.

From the orbit back to the posterior end of the skull table we frequently find in early labyrinthodonts a row of four elements normally termed postfrontal, intertemporal, supratemporal and tabular. All may vary in their anteroposterior dimensions, and the intertemporal frequently disappears. Säve-Söderbergh would explain this by introducing a hypothetical fifth element into the series and assuming varied types of fusion between the five. But never are there five elements present, and the facts are simply explained by variation in extent of ossification of the bones present, and reduction and loss of the intertemporal.

PALATAL STRUCTURE

The lateral margins of the skull, when seen in palatal aspect, are formed by the ventral edges of the marginal roofing elements. These include premaxilla, maxilla, quadratojugal, and often the jugal as well. The last three are concerned in forming the lateral wall of the subtemporal fossa; the jugal may enter onto the palatal plate and brace the ectopterygoid or pterygoid laterally. The maxilla and premaxilla bear the marginal tooth row; their palatal exposure is often little more than the area necessary to bear the row of tooth sockets. However, the premaxilla may have a palatal expansion of modest size, and in cases where the choana is somewhat more medially situated than usual, the maxilla may extend inward to maintain contact with its borders.

The marginal dentition always consists of a single row of teeth. In all cases where the structure is well known, these teeth are labyrinthine in nature. Bystrow (1938a) has given a detailed account of the structure and emplacement of such teeth, based on *Benthosuchus*. Replacement, where material is sufficient to give evidence, seems to be by alternating waves similar to the conditions described in living reptiles and in the pelycosaurs (Romer and Price 1940, pp. 91–93). In consequence we seldom find a full complement of teeth; in one or more regions of the upper jaw there is generally present a condition in which every alternate tooth socket is empty, and in other regions well-preserved specimens show that alternate teeth belong to older and younger tooth generations. In many forms, particularly among rhachitomes and stereospondyls, the tooth row tends to be nearly uniform throughout its length and the teeth small and numerous. There are, however, many variations. In ichthyostegals and anthraco-

saurs the premaxillary teeth tend to be few in number and of large size. In many of the older genera there is a tendency for development of relatively large teeth in the anterior part of the maxillary series after the fashion of the "canine" development in later synapsids etc.; there is not improbably a direct phyletic connection between the reptilian canine development and the amphibian condition.

The general palatal construction of primitive labyrinthodonts can be readily derived from that of crossopterygian fishes. Its elements are of two types: dermal bones, including pterygoid, vomer (prevomer), palatine and ectopterygoid (transverse); and ossifications in the deeper-lying palatoquadrate cartilage — epipterygoid and quadrate. The anterior palatal structures form an essentially flat plate roofing the mouth region, notched laterally for the nares and terminating posteriorly at a transverse flange on the pterygoid. Laterally (externally) the anterior dermal elements are in contact with the marginal dermal bones for most of their extent; the contact is broken for the opening of the choana. Medially the two palatal plates meet anteriorly; more posteriorly they are separated by the interpterygoid vacuities. The posterior end of the interpterygoid vacuity is marked by the basal articulation between palate and braincase. This region is approximately opposite the pterygoid flange referred to above. Posterior to this point the palatal complex twists from a horizontal position to become a vertical plate of bone which curves backward and outward, medial to a large subtemporal fossa for the jaw muscles, to end at the area of articulation for the lower jaw.

Dorsally the anterior region of the palatal structures is subjacent to the anterior end of the braincase and the nasal capsules. Above the region of the basal articulation the palatal complex may articulate with the skull roof by way of the epipterygoid; more posteriorly there may be an attachment to the otic region of the braincase. Posteriorly there is typically a broad union with squamosal and quadratojugal at the rounded posterior margin of the cheek region.

Vacuities are frequently present in the anterior part of the palate in rhachitomes, either as paired openings or a single, sometimes bilobed, structure, typically lying along the premaxillary-vomerine suture. Living amphibians have prominent intermaxillary glands in this region and these vacuities are generally believed to be associated with those structures. I tend, however, to believe that the development of symphysial tusks is in general responsible for the presence of these vacuities. Their development is correlated with (1) the

length of the symphysial fangs and (2) the height of the palatal roof above the level of the jaw symphysis when the mouth is closed. These vacuities are thus most likely to occur when large symphysial tusks are present in flat-skulled forms — a condition most common in stereospondyls.

The choana typically occurs just within the maxilla and premaxilla, adjacent to the marginal tooth row, with the anteromedial margin formed by the vomer, the posterior margin by the palatine. In anthracosaurs the choanae are typically placed rather anteriorly and medially, and thus relatively close together; in temnospondyls they are relatively widely separated and more posteriorly placed.

In almost all Paleozoic amphibians there is present a pair of interpterygoid vacuities, separated in the midline by the cultriform process of the parasphenoid and bounded laterally by the pterygoid and usually by other palatal elements as well. In anthracosaurs they are always small and sometimes (as in *Seymouria*) nonexistent. This situation also prevails in the early ichthyostegids and other primitive temnospondyls and is reasonably to be considered a primitive one, but in advanced types the openings reach an enormous development, to occupy the greater part of the palatal surface; a functional advantage appears to be a decrease in the "dead weight" of the skull by the elimination of useless bone. As first clearly pointed out by Watson, this tendency toward development of large vacuities was a common one throughout the labyrinthodonts. The vacuities are uniformly small in early members of all groups, but had expanded in parallel phylogenetic fashion in later ichthyostegids, rhachitomes and stereospondyls and even (to a minor extent) in the late seymourian *Kotlassia*. Similar expansions of the vacuities took place among amphibian groups beyond the boundaries of the Labyrinthodontia, for they are widely open in the late nectridian *Diplocaulus*, in the modern urodeles and in the Anura and their ancestors.

In most cases teeth are highly developed on the dermal palatal elements. Most noteworthy is the presence of paired fangs of large size. A fang-pair is frequently found in specimens in a condition in which one member of the pair is represented by a well developed tooth, the other by a replacement pit or small developing tooth. Apparently here, much as in the marginal teeth, there was a functionally efficient alternating type of tooth replacement. Fang-pairs appear to have been situated, one pair to an element, in many early forms, on vomer, palatine and ectopterygoid. The vomerine pair is usually placed just anterior to the choana and is unreported in

the anthracosaurs; the palatine pair just posterior to the choana; the ectopterygoid pair near the anterior end of that element.

In a number of forms, particularly advanced rhachitomes and stereospondyls, the fang-pairs may be supplemented or replaced by rows of teeth of more modest size. Such rows may be found crossing the anterior part of the palate between the two vomerine fang-pairs; running between vomerine and palatal pairs along the inner margin of the choana; and extending from the palatine pair back along the length of palatine and ectopterygoid. When such rows of teeth are developed, the fang-pairs may undergo reduction as if the development of such a row consisted in fragmentation of the major structures. The primary ectopterygoid pair is frequently reduced, the palatal pair less frequently; the vomerine pair almost always persists.

In addition to the types of teeth described, the dermal palatal elements (including the pterygoid) may carry a shagreen of small denticles in many cases; I have not indicated them in the figures of palates given here. In many forms their presence or absence is uncertain, since they are liable to be destroyed in the preparation of specimens. Such small teeth appear to have developed more or less independently of the bones beneath them, and in some cases (as, for example, *Stegops*) may have developed in the skin of the roof of the mouth beneath the palatal vacuities as well as beneath the adjacent palatal bones.

The vomer (prevomer) is typically a fairly large subquadrate bone meeting its fellow in the mid-line. The vomer is bounded anteriorly and laterally by the curving premaxilla; posteriorly it meets the palatine and, primitively, the pterygoid. Posteromedially the vomer has a variable relationship with the cultriform process of the parasphenoid. Dorsally the bone was presumably in contact with the floor of the cartilaginous nasal capsule. With the development of large interpterygoid vacuities the vomers tend to enter into their borders and to lose contact with the dwindling pterygoids. In many anthracosaurs the choanae, as noted, are rather anteriorly placed and relatively close together, so that the vomers are narrow bar-like structures, resembling those of reptiles. In rhachitomes and stereospondyls, where the choanae are frequently placed in a relatively posterior position, the vomers have tended to follow them and to gain contact with the maxillae at the anterior margin of the choanae.

The palatine is a lateral dermal element, lying along the inner margin of the maxilla between the choana and the ectopterygoid. Medial to the choana the palatine is in contact with the vomer.

Primitively the palatine was bounded medially by the pterygoid; with the enlargement of the interpterygoid vacuities in advanced types, the palatine becomes a relatively slender element lying along the lateral margin of the vacuity, frequently losing contact with the pterygoid. The palatines are thin medially, but laterally tend to thicken in buttressing the palate against the maxilla and, in some cases, at least, may extend upward under more dorsal elements of the roofing series. The dorsal aspect of the thickened lateral region is seen in some instances to be penetrated by a varied series of openings. These have been considered as having been occupied in life by cartilaginous processes of the nasal capsule but appear to have been, in part, at least, related to the passage of blood vessels and nerves.

The ectopterygoid is essentially comparable to the palatine but of smaller size, lying medial to the maxilla and lateral to the pterygoid. Anteriorly it is bounded by the palatine; posteriorly it may border the subtemporal fossa. At its posterior margin however it may be braced by an inward extension of the jugal which excludes it from the boundary of the fossa. Like the palatine, it may enter the margin of the interpterygoid vacuities when these openings are enlarged.

Most prominent of palatal structures is the pterygoid, which extends in primitive forms nearly the entire length of the skull as a dermal complement to the embryonic palatoquadrate cartilage. It may be considered as consisting of three components: an anterior, horizontally expanded palatal ramus, a posterior, vertically placed quadrate ramus and, between the two, a thickened central area in the region of the basal articulation with the braincase.

The palatal ramus is, in primitive forms, a greatly expanded sheet of bone covering much of the palate. In such forms the pterygoid meets its fellow of the opposite side anterior to the interpterygoid vacuities, ventral to the tip of the parasphenoid. The medial border of the pterygoid primitively forms the lateral margin of the vacuities. Anteriorly, in a primitive condition, the pterygoid is in contact with the vomer, laterally with the entire length of the palatine and ectopterygoid. The posterior margin of the palatal ramus is typically somewhat thickened and turned ventrally to form a flange at the anterior edge of the subtemporal fossa; this flange, however, is never as highly developed as is the case in typical reptiles with the "rhynchocephalian" type of palate. In some large forms (as *Edops*, *Capitosaurus*) the pterygoid may exhibit rugosities comparable to those seen on the dermal elements of the outer surface of the head. The dorsal surface of the palatal ramus, where exposed and well preserved, may

be seen to bear markings defining the margins of the cartilaginous anterior portion of the palatoquadrate.

In the development, in many lines, of large interpterygoid vacuities, the palatal ramus of the pterygoid is seen to be progressively reduced. In but relatively few cases is the anterior connection between the two pterygoids preserved. With moderate development of the vacuities the pterygoid may retain a connection with the vomer, but be reduced

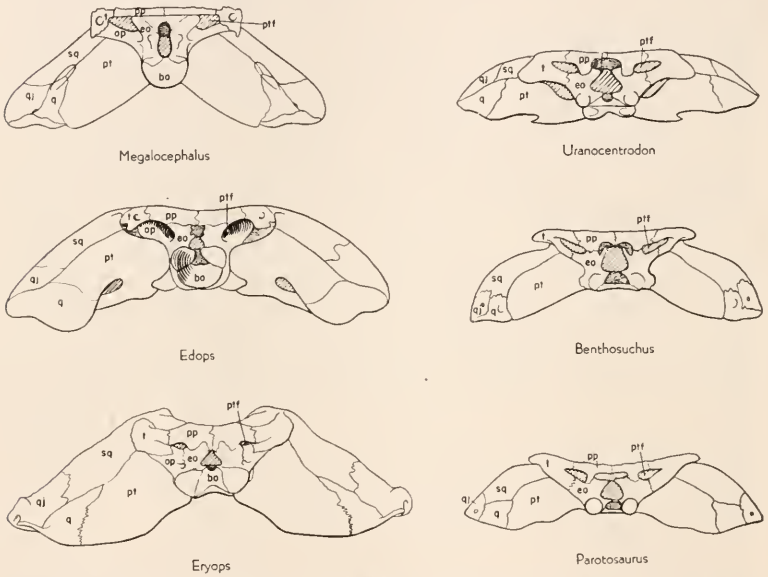

Fig. 2. Posterior views of skulls. *Megalocephalus* after Watson; *Uranocentrodon* after Broom and Haughton; *Benthosuchus* after Bystrow and Efremov; *Eryops* after Sawin; *Parotosaurus* after Watson.

to a relatively small strip of bone lateral to the vacuity. With further growth of the opening, the pterygoid is frequently confined to the posterior portion of the palate and loses contact successively with vomer and palatine.

The central region of the pterygoid (Figs. 2–6) (in which lies its center of ossification) is a much thickened area lying opposite the basisphenoid region of the braincase (Figs. 5, 6). The lateral (morphologically internal) surface of this region is covered by the central portion of the apposed epipterygoid. Primitively (as far as our

evidence goes) this area of the pterygoid is in part formed around and fused with a portion of the epipterygoid to bear a deep socket for articulation with the basipterygoid process of the basisphenoid; generally no line of suture between the two elements is visible in the area surrounding this socket.

Some difficulty is encountered among the more primitive rhachitomes, particularly in crushed material, in determining the nature —

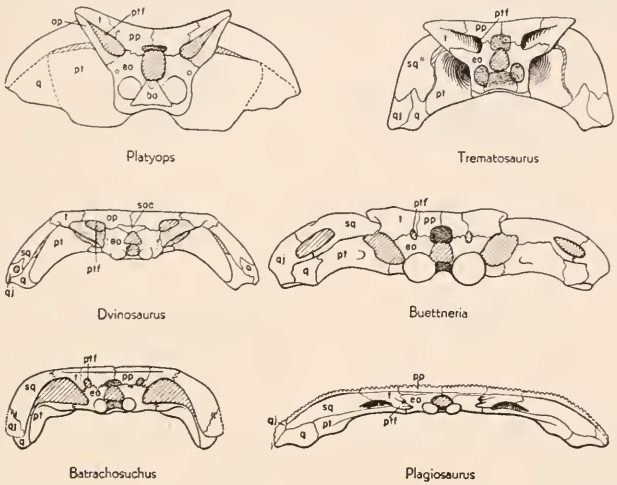

Fig. 3. Posterior views of skulls. *Platyops* after Efremov; *Trematosaurus* after Jaekel; *Dvinosaurus* after Bystrow; *Buettneria* after Case, Wilson; *Batrachosuchus* after Watson; *Plagiosaurus* after Huene.

movable or fixed — of the basal articulation. Unless the cartilage replacement bones are well ossified beneath them, parasphenoid and pterygoid may separate *post-mortem* even though palate and braincase were fused in life. This difficulty is most commonly encountered in dealing with young individuals. As the "branchiosaurs" witness, the dermal palatal elements tend to fall away from the braincase in cadavers of larvae even though we know from adult specimens that the joint was immobile.

In forms, such as *Edops* and the anthracosaurs, in which the basal articulation here between braincase and palate retains its primitive motility, the pterygoid does not appear to enter greatly into the actual articulation, which is mainly one between the apposed endo-

chondral elements — epipterygoid and basisphenoid. However, the pterygoid forms a boundary for the socket anteriorly, ventrally and posteriorly, and is close to a contact in this region with the parasphenoid, which sheathes the basipterygoid process. In such a form as *Eryops,* in which motility is lost and braincase and palate are fused, but in which the connection is a narrow one, much of the junction between palate and braincase may still be carried by the epipterygoid. However, the pterygoid has entered definitely into the joint by sutural union with the apposed surfaces of the parasphenoid anteriorly,

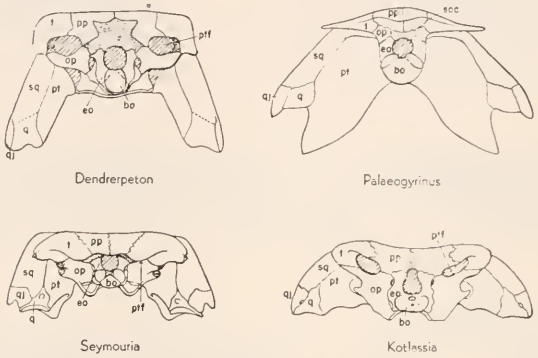

Fig. 4. Posterior views of skulls. *Dendrerpeton* after Steen; *Palaeogyrinus* after Watson; *Seymouria* after White; *Kotlassia* after Bystrow.

ventrally and posteriorly around the endochondral core. In such a neorhachitome as *Benthosuchus* the pterygoid articulation with the parasphenoid is much elongated antero-posteriorly along the flattened palatal surface. The line of union of pterygoid and parasphenoid no longer extends upward anteriorly, but does rise posteriorly into a thicker appositional area back of a cavity in the pterygoid which has been termed the "conical recess". In these forms the reduced epipterygoid appears to have withdrawn from the articulation. The pterygoid has taken over the socket area for reception of the basisphenoid in the form of this recess which, in position, shape and apparent function, seems exactly equivalent to the cavity seen in the freely movable articulation of *Edops.* Comparable conditions are seen in trematosaurs.

In the neorhachitomes the area of contact between pterygoid and parasphenoid is greatly elongated antero-posteriorly; posteriorly the

line of contact between pterygoid and braincase floor becomes so extended that the exoccipital may join in its formation, although this latter union is not generally visible from the ventral surface. In typical Triassic temnospondyls the length of the suture between pterygoid and braincase is further increased. In capitosaurs in general the structure is otherwise closely comparable to that in neorhachitomes; in the trematosaurs the union is, in surface view, one purely between pterygoid and parasphenoid, although the latter element extends remarkably far back. In metoposaurs there is less posterior expansion of the parasphenoid and there is visible ventrally a broad contact of pterygoid with exoccipital.

The deeper region of the contact is seldom seen in advanced Triassic temnospondyls. Where well known there is, as in neorhachitomes, a thickened surface of apposition on the pterygoid posterior to the position of the primitive basipterygoid articulation. In metoposaurs, at least, the epipterygoid appears to have persistently taken some part in the basal contact, but between the epipterygoid and the posterior thickening just mentioned there is, again, a conical recess comparable to that of neorhachitomes and obviously for the reception of the basipterygoid process.

The quadrate ramus of the pterygoid extends posteriorly and laterally from the region of the basal articulation as an essentially vertical sheet of bone. Ventrally it may extend downward a considerable distance as a median sheath for the jaw muscles. Dorsally it rises high above the level of the basal articulation and lies close to the lateral margin of the otic capsule, although it is apparently not primitively in contact with it. At the level of the anterior margin of the otic notch the upper margin of the ramus comes in contact with the squamosal, and this contact continues postero-laterally to give, in most cases, a continuous posterior wall to the cavity containing the jaw musculature. The nature of the articulation with the squamosal is variable and the details are often obscure. The pterygoid may, for example, overlap medially and posteriorly a descending process of the squamosal, and in metoposaurs this postero-medial flange forms a structure (the "posterior rising process" of Case and of Wilson) which is more or less independent of the primary quadrate ramus ("anterior rising process"), the two apparently embracing the squamosal flange. Laterally the pterygoid terminates in a suture with the quadrate, which it tends to overlap postero-medially. The lateral (morphologically internal) surface of the quadrate ramus was in great measure covered by the epipterygoid in primitive forms, in

more "advanced" types by the posterior wing of the palatoquadrate cartilage. In all well-known forms the medial surface of the pterygoid bears a deep pocket posterior to the articular region; it is, for example, seen typically in forms as far separated as *Edops*, *Benthosuchus*, and *Buettneria* and is also present in early reptiles. Bystrow has suggested that its presence is related to the middle ear cavity, and termed it the "excavatio tympanica"; Wilson, on the other hand, believes it developed in relation to muscle insertion. The lower margin of the quadrate ramus is frequently turned medially in an essentially horizontal plane. This flange is present also in some primitive reptiles and may have formed a floor for the middle ear cavity.

The embryonic palatoquadrate cartilage appears to have been highly developed in early amphibians. Anteriorly it presumably was in contact with the nasal capsule structures; in mid-course it articulated basally with the basipterygoid process of the braincase and sent up an ascending process toward the skull roof; posteriorly it rose to gain an otic contact with the ear capsule, and at its distal end articulated with the lower jaw. In labyrinthodonts two ossifications typically occur in this cartilage, epipterygoid and quadrate. Primitively these replaced, in the adult, the greater part of the embryonic cartilage, but in young individuals or small types they are often feebly developed, and phylogenetically there is a strong trend toward reduction in the degree of ossification.

No instance is known in which the anterior end of the cartilage is ossified, although impressions of its presence have been noted far forward on the upper surface of the dermal palatal elements which sheathed it. Attempts have been made to restore the connections of the palatoquadrate cartilage with the likewise cartilaginous nasal capsule, but these are almost entirely hypothetical. Säve-Söderbergh (1936, pp. 42–43, 151, etc.) has restored a complicated set of connections here by comparison with the larva of *Rana*, but Pusey (1938) points out that this is a highly specialized larva of a highly specialized frog, and that radically different conditions would be expected in a non-anuran adult.

The epipterygoid, the more anterior of the two ossifications in the palatoquadrate, appears to have extended far forward above the palate in primitive types, but there is little available evidence. In such a moderately advanced form as *Eryops* this anterior, palatal, process of the epipterygoid is much reduced, and in more advanced types the entire anterior wing of the palatoquadrate is cartilaginous.

The most persistent portion of the epipterygoid ossification lies in the region of the basal articulation. Here the bone is relatively thick in such a form as *Edops* and, fusing with the adjacent part of the pterygoid, it forms a deep socket into which was inserted, with a movable articulation, the basipterygoid process of the braincase. In such a type as *Eryops*, where the articulation has become immovable but is still restricted in extent, the socket still persists. In trematosaurs and capitosaurids the epipterygoid appears to have retreated from the socket, "the conical recess" in the pterygoid. In metoposaurs, however, the epipterygoid appears to have still shared in the braincase articulation, for although the pterygoid bears a recess for the tip of the presumed basipterygoid process there is, adjacent to this recess, an articular area on the inner aspect of the epipterygoid which may well have been in contact with part of the basipterygoid process.

Above the region of the basal articulation the epipterygoid has, in every case studied, a well developed ascending process which in many forms reaches nearly to the skull roof just lateral to the braincase. As is known from its persistence in living reptiles (as the columella cranii) it is a useful morphological landmark separating the ophthalmic division of the trigeminal nerve, which passes forward medially to this structure, from the second and third divisions of this nerve, which turn laterally posterior to it. The epipterygoid is not primitively in contact with other elements dorsally, although it was presumably in connection by either ligaments or cartilage with the skull roof. In trematosaurs it is believed to have turned sufficiently inward to gain a contact with the lateral wall of the braincase region. It is thought that posterior to this region the embryonic cartilage spread out widely dorso-ventrally over the inner surface of the pterygoid — or, rather, the pterygoid has developed superficially over the area occupied by the embryonic cartilage. That this is the case appears to be proved by the fact that in *Edops* the epipterygoid is very widely ossified here as a broad sheet which comes into contact with the quadrate and, with that element, appears to have practically completely replaced the embryonic structure.

Distinct from, but closely parallel posteriorly to the "columella", the epipterygoid rises to an otic process which in favorable cases is seen to gain a definite although limited contact with the lateral wall of the otic capsule.

The high development of the epipterygoid in *Edops* is presumably primitive; it is not repeated in more "advanced" types, although the

cartilage from which it arises was probably persistent. In *Eryops*, for example, there is a broad development of the bone at the level of,

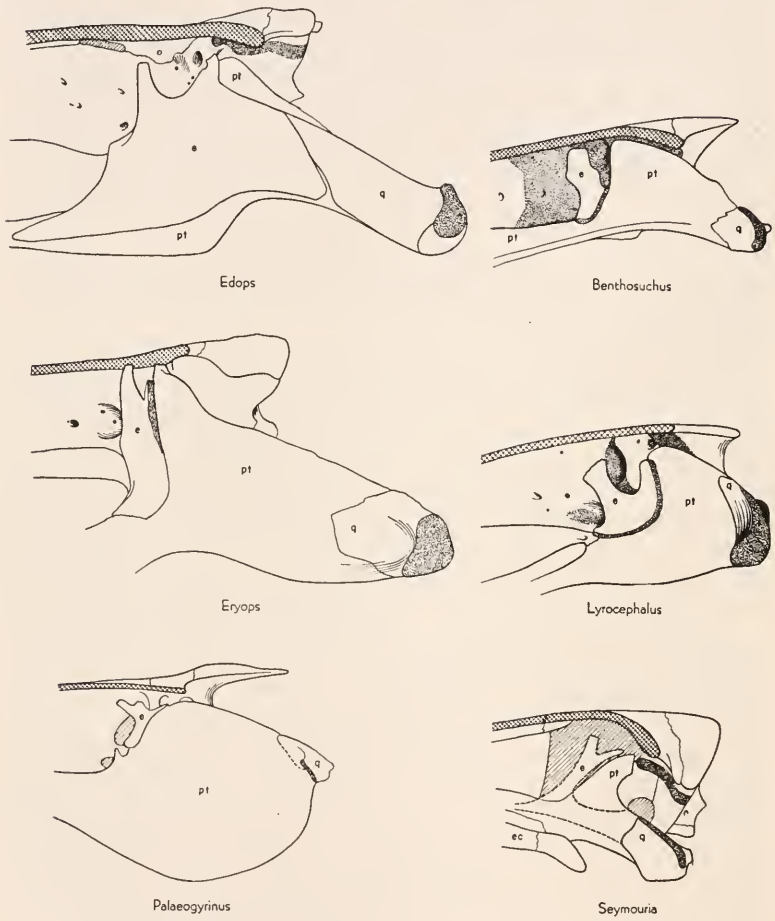

Fig. 5. Comparative external views of left palato-quadrate complex of various labyrinthodonts; diagrammatic, and freely restored. Presumed structures and areas in cartilage, stippled. Cross-hatching refers to bone sectioned. Data for figures 5 to 8 have been derived as follows: *Edops* after Romer and Witter; *Eryops* after Sawin; *Benthosuchus* after Bystrow; *Lyrocephalus* after Säve-Söderbergh, partly based on *Aphaneramma* and *Trematosaurus*; *Palacogyrinus* after Watson; *Seymouria* after White.

and including, the otic process, but there is a considerable gap behind this region between epipterygoid and quadrate. In more "advanced" temnospondyls, there may be a small otic process, or even this may

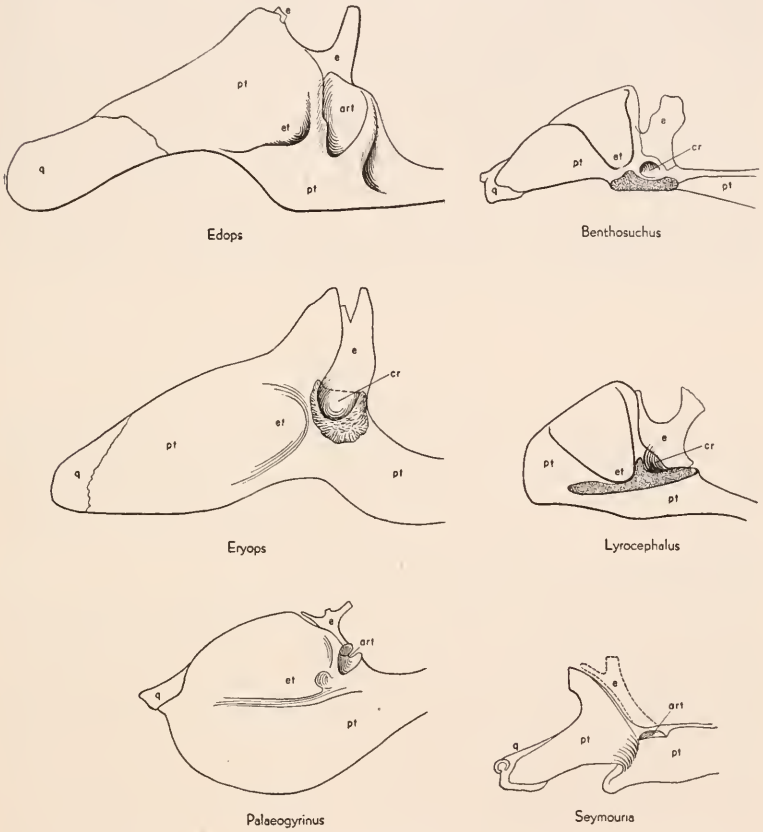

Fig. 6. Median views of left palato-quadrate complex of forms seen in figures 5, 7, 8.

be absent and the bone consist merely of the columella and a small basal area beneath it.

Related to its important function as the articular element for the jaw, the quadrate is a constant and persistent structure. There is always present a thickened portion, placed in a transverse plane

between pterygoid and quadratojugal, which bears the articular surface; this surface is convex and tends to be doubly keeled. Laterally the bone abuts broadly on the inner surface of the quadratojugal; medio-dorsally the quadrate tends to extend, as a relatively thin flange, along the inner surface of the overlapping pterygoid, toward or to a contact with the epipterygoid. Dorsally this ramus is in contact with both quadratojugal and squamosal. Near the boundary between quadrate and quadratojugal there is, apparently generally, a foramen passing forward into the temporal muscle fossa. In some cases this foramen lies in the suture between the elements and has been termed the quadrate foramen; in others it lies more in the quadratojugal and in consequence the term "paraquadrate foramen" has been suggested by Bystrow as more appropriate. An accessory foramen may also be present in this region.

PARASPHENOID

In labyrinthodonts, as in bony fishes and all primitive land vertebrates, the braincase is ensheathed ventrally by a median dermal element, the parasphenoid. In many forms we know little of the nature of the braincase itself, and much of our knowledge of its structure is inferred from that of the parasphenoid; this element, therefore, is one of considerable importance.

The body of this bone broadly encases ventrally the stout posterior portion of the braincase; an elongate cultriform process extends forward beneath the narrow sphenethmoid portion of the braincase. In some areas, such as part of the lateral walls of the cultriform process and the postero-lateral margins of the body of the bone, the boundaries of the parasphenoid are readily seen in most cases. In other areas, however, the parasphenoid blends gradually into the periosteal bone sheathing the braincase and is difficult to delimit.

The cultriform process is primitively narrow in ventral view and V-shaped in section, sheathing the originally narrow ventral margin of the overlying sphenethmoid. In advanced labyrinthodonts the process tends to be broader and flatter, most notably in metoposaurids. The anterior end of the process primitively extended forward dorsal to the anterior ends of the conjoined pterygoids and vomers. With withdrawal of the pterygoids from the midline, and with flattening of the skull, the cultriform process of the parasphenoid comes to lie in the plane of the anterior palatal structures and to articulate with

the paired vomers by a V-shaped terminal process wedged in between them.

At the posterior margin of the interpterygoid vacuities the parasphenoid (Figs. 7, 8) expands laterally to sheath much of the extent of the basipterygoid processes of the basisphenoid. In primitive forms, where the process is movably articulated with the palatal structures, the lateral margin of the parasphenoid sheathes its basisphenoidal core ventrally, anteriorly and posteriorly, but takes no great part, apparently, in the actual articulation. In such a form as *Eryops*, in which the articulation with the upper jaw structure is a fixed one but the articular region narrow, the configuration of the parasphenoid is similar. Here, however, the bone enters actively into the union, forming a sutural connection with the pterygoid and ensheathing the basal core of basisphenoid anteriorly and posteriorly as well as ventrally. In lateral view, when disarticulated, this sutural surface of the parasphenoid is seen to be crescent-shaped, with anterior and posterior ascending "horns".

In neorhachitomes the shape of this articulation has changed greatly. The extent of the parasphenoid-pterygoid contact has been much increased, mainly in a posterior direction. The sutural surface, as seen in lateral view, is thus relatively low dorso-ventrally, but elongate antero-posteriorly. The upturned "horns" of the original crescentic structure are absent as such. However, a pair of thickened areas extends dorsally from the general plane of the parasphenoid plate. One of these thickenings lies close to the anterior termination of the contact area; the second one some distance posterior. Opposite the gap between these two processes there lies, on the pterygoid, the conical recess which received the basipterygoid process of the basisphenoid. These thickenings are thus closely comparable with the horns of the crescentic articular surface seen in *Eryops*. On the dorsal surface of the parasphenoid a thickened ridge passes backward and outward from the center of the bone to the more posterior of these processes.

In Triassic stereospondyls the general configuration of the articular area is much the same, as far as it is known, but the length of the articulation tends to increase further in a posterior direction.

In primitive forms the parasphenoid passed back as a narrow sheet of bone in a constricted area between the basipterygoid processes, and then spread out broadly, with rounded contours, to ensheath much of the ventral and ventro-lateral surfaces of the braincase. In more advanced labyrinthodonts, in which the braincase (and the

skull in its entirety) becomes greatly broadened and flattened, this whole region of the parasphenoid becomes a very broad and flat sheet of bone. In primitive types paired posterior folds of the parasphenoid, together with underlying endochondral bone, form basisphenoidal tubera for the ventral neck muscles. In advanced temno-

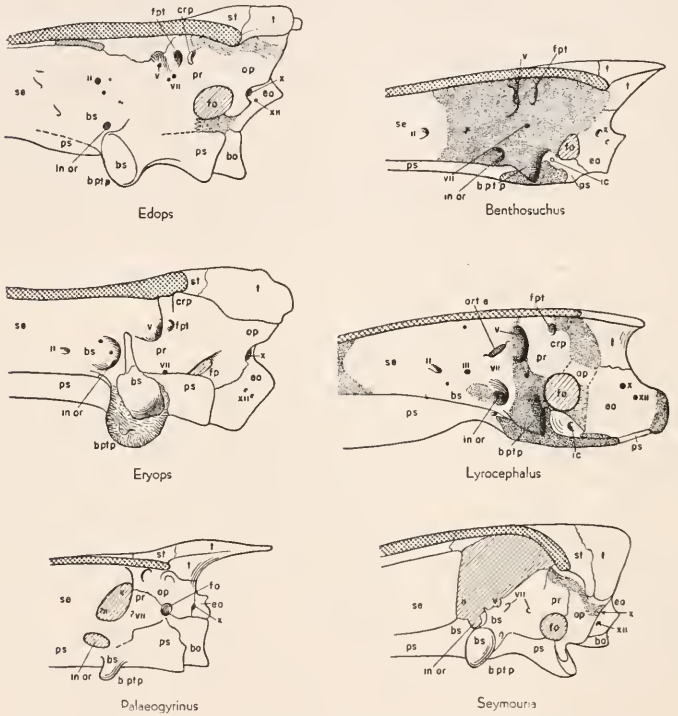

Fig. 7. Left lateral view of braincase of forms seen in figures 5, 6, 8.

spondyls with flattened palates these tubera tend to be reduced or absent.

In all primitive tetrapods, and in bony fishes, the internal carotid arteries run forward beneath the braincase median to the basipterygoid processes to a point anterior to these structures and to the pituitary fossa, and then pass upward into the braincase. In this forward passage their relations with the parasphenoid are variable. In *Eryops*, for example, the arteries are superficial in position for most of their

course forward and upward about the base of the basipterygoid processes although their position may be marked by well defined grooves; they enter the parasphenoid only at a point directly below that at which they pierce the basisphenoid to enter the brain cavity. This superficial position appears to be associated with a relative reduction in the development of the parasphenoid, for *Edops* shows a condition, apparently duplicated in many Carboniferous forms, in which the carotid enters a canal far back in the parasphenoid and runs forward continuously in the substance of that bone to the point at which it turns dorsally to leave the parasphenoid and pierce the basisphenoid. In neorhachitomes increased development of the parasphenoid has, so to speak, enmeshed a further section of the carotid. It now enters the bone far postero-laterally and close to the pterygoid suture. It passes forward some distance in the substance of the parasphenoid and then, apparently, continues further to its basisphenoid entrance between the parasphenoid and the surface of that bone; its course may be indicated by a groove on the dorsal surface of the parasphenoid. This condition is also present in other Triassic stereospondyls and in trematosaurs.

The internal carotid typically gives off a prominent branch, the palatal artery, some distance back of its point of entrance into the braincase. In both *Eryops* and *Edops* this artery is entirely superficial to the parasphenoid, although in the latter its position is marked by a groove in the parasphenoid beneath the basipterygoid process (Romer and Witter 1942, fig. 11A, PAG). In neorhachitomes (Bystrow and Efremov 1940, fig. 10, *rp*) the posterior part of this artery is enclosed in the bone; more anteriorly it lies in a canal formed by a groove on the upper surface of the parasphenoid and, of course, enclosed dorsally by the surface of the basisphenoid. In metoposaurs and trematosaurs there is present a canal in the antero-lateral portion of the parasphenoid which Säve-Söderbergh (1936) and Wilson (1941) believe to have transmitted the palatine branch of nerve VII. In *Lyrocephalus*, where the canal is seen to enter the bone dorsally and leave it anteriorly, this interpretation might be possible. But in other cases there is no separate point of entrance into the bone for this canal, and it cannot have carried this nerve. It seems rather obvious that we are here also dealing with a canal for the palatal artery, branching within the parasphenoid from the carotid canal.[1]

[1]A groove on the lower surface of the parasphenoid in trematosaurs has been interpreted as the course of this artery; but this extremely superficial position is highly improbable, and this groove is more reasonably regarded as for a vessel associated with the mucous membrane of the mouth or pharynx — for example, a posterior branch of a medial palatine vain such as that of the frog.

In many cases, and perhaps generally, in the more primitive genera, the upturned postero-lateral corner of the parasphenoid forms part of the margin of the fenestra ovalis, or at least closely approaches the

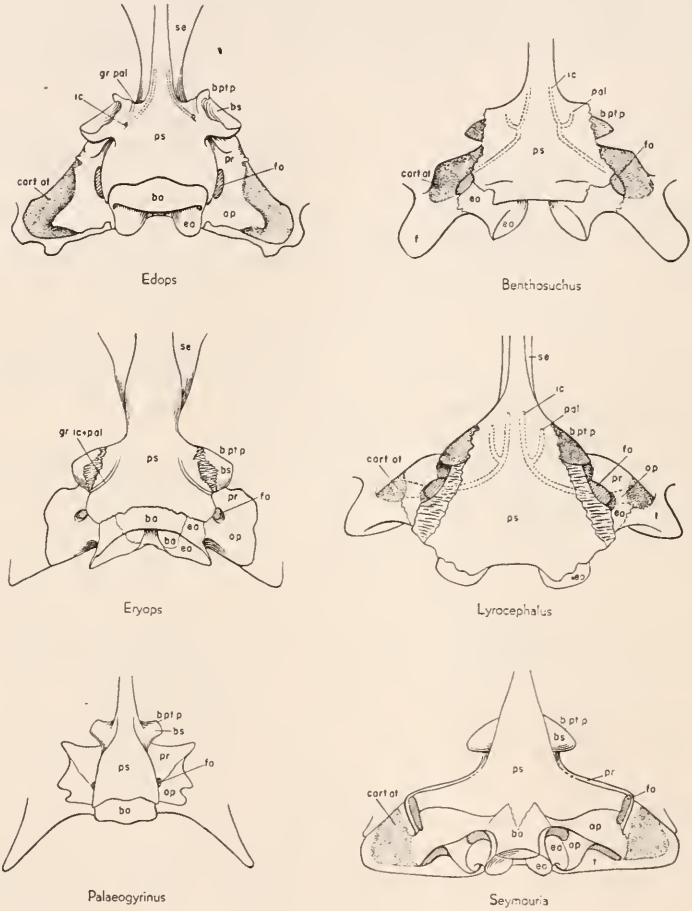

Fig. 8. Ventral view of braincase of forms seen in figures 5 to 7.

actual margin formed by the underlying endochondral bone or cartilage. This condition persists in other late types as well.

The posterior portion of the parasphenoid in most early forms was a relatively thin, curved sheet of bone sheathing the basioccipital

ventrally and laterally, and with a free posterior margin. However, in most temnospondyls the posterior portion of the parasphenoid becomes flattened, tends to lose its free posterior margin, and, lying in a plane with the ventral surface of the exoccipital, acquires a powerful terminal sutural union with that bone in most stereospondyls. In trematosaurs, however, the suture is absent; the flattened parasphenoid extends backward to cover most of the ventral surface of the exoccipital.

BRAINCASE

(Figs. 2–4, 7, 8)

Our knowledge of the braincase is limited. In many cases we know nothing at all of its structure; in most other cases we know, at the most, such few features as can be seen from the ventral and occipital aspects. Only in a relatively few forms has there been any adequate description given, and even here our knowledge is restricted in the case of later Permian and Triassic genera by the fact that much of the braincase had been cartilaginous and hence has not been preserved. Of forms which are relatively well known we may cite: certain embolomeres (Watson 1926); *Seymouria* (White 1939); *Kotlassia* (Bystrow 1944); *Edops* (Romer and Witter 1942); *Eryops* (Sawin 1941); *Benthosuchus* (Bystrow and Efremov 1940); certain Triassic genera (Watson 1919); trematosaurs (Säve-Söderbergh 1936).

The general architecture may first be noted. From its posterior end at the foramen magnum and occipital condyle (or condyles), the braincase, followed forward, almost immediately reaches its greatest expansion and extends far laterally in the otic region; thence it constricts to a "waist" at the level of the pituitary fossa and basal articulation. From this point forward there is a gradual expansion in breadth as far as ossification is present in the ethmoidal region. The most anterior portion of the braincase, including the nasal capsules, is never ossified, although one may infer that structures here were well developed. Primitively the braincase appears to have been relatively high and narrow, as in the fish ancestors and in reptilian descendants. In advanced temnospondyls, however, there is a tendency toward a flatter, broader structure of the embryologically platybasic type.

Dorsally the braincase is closely applied to the under surface of the dermal bones, and these bones may also overlap the occipital surface to a variable degree. The details of the upper surface are known in but few cases. In some (as *Edops*, *Eryops*, *Palaeogyrinus*)

the upper surface may have been nearly complete, with, however, a fontanelle over much of the fore- and midbrain regions; in more advanced forms there is relatively little ossification of the dorsal surface, and we have no exact knowledge of the degree of development of a cartilaginous skull roof.

Laterally, we have noted contacts, of relatively slight functional importance, between the otic region and the pterygo-quadrate apparatus. Farther forward and ventrally is the basal articulation, of great importance both structurally and functionally. It is possible that the epipterygoid may have articulated with the braincase as well as the skull roof in this region in some types.

As noted, much of the ventral surface is sheathed by the parasphenoid. Anteriorly the cartilaginous nasal capsules were obviously applied to the dorsal surface of the palatal structure — specifically the vomers.

The braincase in primitive forms was highly ossified (much as in the ancestral fishes), except for the nasal capsules and the most anterior part of the braincase proper. In advanced temnospondyls we find a progressive trend toward a retention of cartilage in the adult and a consequent reduction in ossification.

In primitive forms there is not only a nearly complete ossification but an almost complete lack of visible sutures in mature specimens (a condition comparable to that of crossopterygians). As a consequence little can be determined as to the bony elements which form the braincase. As reduction of ossification proceeds, however, there is a gradual emergence of discrete elements which may be assumed to have been present in the older types. These appear to be capable of grouping into a number of regions — occipital, otic, sphenoid and ethmoid. The first two of these four regions may be considered to form a larger otico-occipital unit, the last two an ethmo-sphenoid unit; it is of interest with regard to amphibian origins that these two units correspond not only to the embryological parachordal and trabecular regions of the early embryo, but to the two discrete structures of the adult crossopterygians. It appears probable that in anthracosaurs the sutures were more generally visible; this, together with the presence of an interorbital septum, and a consequent gap in ossification, makes the regional subdivisions apparent.

The occipital region, in a proper sense, is the central portion of the area seen in occipital view, including the area surrounding the foramen magnum and the occipital condyle(s) below it. Primitively the condyle is a single subcircular structure, with a raised rim and con-

cave center, in which there may be a notochordal pit. The central part of the condyle is formed by the basioccipital bone, the upper lateral portions by the exoccipitals. This type of condyle is present in very primitive temnospondyls (as loxommids, *Edops*, *Dendrerpeton*) and in embolomeres and seymouriamorphs.

In advanced temnospondyls, however, there tends to develop a double condyle, facilitating dorso-ventral (but not lateral) movement of the head. This is a development parallel to that seen in some lepospondyls, in living amphibian orders and, to some extent, in that of the ancestors of the mammals, and it appears probable that it occurred in several independent temnospondyl lines. It is associated in general with a withdrawal of the basioccipital from the condyle, leaving the dorso-lateral areas formed by the exoccipital as the functional condyles. Flattened in many cases, these condyles tend in some advanced types to be rounded hemispherical structures. One transitional type is that seen in *Eryops*, where a strap-shaped band on the basioccipital separates the developing exoccipital surfaces; with the dropping out of the basioccipital, two widely separated condyles remain. In other early Permian genera, as the trematopsids, two nearly distinct articular surfaces may be present, but they are in contact with one another, suggesting an independent and rather different method of evolution.

The basioccipital primitively extends well forward in the floor of the braincase as a wedge-shaped structure, covered below in part by the parasphenoid, bounded laterally by the exoccipitals and (farther forward) the otic capsule elements. In no known case is its upper surface a finished one; a persistently cartilaginous area seems to have been present in the floor of the braincase. In advanced temnospondyls — generally concomitantly with subdivision of the condyle — the basioccipital becomes further reduced, to form a thin ossification on the upper surface of the parasphenoid, and may disappear completely.

The paired exoccipitals form at least the dorso-lateral portions of the condylar area; thence they extend forward along the side wall of the braincase to the large foramen carrying the vagus nerve and associated structures, and upward along the lateral margins of the foramen magnum. The inner surface of the exoccipital forms the lateral wall of the braincase in the post-vagal region. Ventrally it exhibits an internal shelf which formed a partial floor to the medullar region, overlying the cartilage mentioned above in connection with the basioccipital. The lateral wall is reported in various older or

more primitive genera to be pierced by one or two foramina for the twelfth (hypoglossal) nerve. This is clearly a primitive tetrapod character, and one already present in crossopterygians (Romer 1937); the absence of the nerve in modern amphibians and, apparently, in a considerable percentage of the labyrinthodonts is a secondary condition. In some instances the posterior surface of the exoccipital bears, as in many primitive reptiles, a facet for the proatlas.

The exoccipital area so far considered is essentially that of the cartilaginous occipital arch of the embryo, and in reptiles generally the exoccipital has no further extension. Laterally, the exoccipital primitively appears not to have passed beyond the vagus foramen, which represents the primitive fissure between occipital arch and otic capsule. A similar condition appears to have been true of embolomeres and seymouriamorphs, as far as known, and in some early temnospondyls a suture in the region of the vagus foramen indicates a similar condition. In most temnospondyls, however, there is a marked reduction in the extent of ossification of the opisthotic bone of the ear capsule, and above the rhachitomous level the exoccipital invades the former area of ossification of the opisthotic.

In reptiles the area above the foramen magnum is occupied by a well-developed bone, termed the supraoccipital (although it should be remembered that this area is the embryonic synotic tectum and not a part of the occipital arch). The conditions in labyrinthodonts are obviously highly varied but are frequently obscure. The area is often covered, in part or whole, by descending flanges of the postparietals; these appear to be purely dermal in nature, without any endochondral component. In many cases amongst both primitive and advanced temnospondyls the central part of this area is unossified and filled by cartilage in life, with the exoccipitals extending upward on either side to meet the postparietals; in other temnospondyls the central region is ossified, but there is little or no evidence of a distinct supraoccipital element. It would thus appear that dorsally, as laterally, the temnospondyl exoccipital has expanded beyond the limits of the occipital arch and has invaded the synotic tectum.

In anthracosaurs, as far as known, the exoccipitals, as in reptiles, do not exceed the limits of the embryonic occipital arch. In every one of the few cases where the structure is clear, the exoccipitals stop short of the dorsal region of the braincase and leave above them a definite supraoccipital area in the synotic tectum. This area was apparently unossified in typical seymouriamorphs, but in some instances a slight ossification is present. In *Palaeogyrinus*, the only

embolomere in which the region has been clearly seen, there is a discrete ossification in the supraoccipital region. It seems probable, on present evidence, that a supraoccipital bone is an anthracosaurian and reptilian feature; it has either appeared in these forms as a new element, or, if present in primitive tetrapods, disappeared at an early date in temnospondyls.

In advance of and lateral to the occiput, the otic capsules, in the form of cartilages and the bony elements replacing them, form a major element in braincase construction. They border much of the brainstem region of the endocranial cavity and enclose the various cavities of the internal ear; laterally the otic capsule projects upward as the powerful paroccipital process to end beneath the tabular at the postero-lateral corner of the skull table. Above this process is the posttemporal fossa. Ventrolaterally the capsule forms most or all of the margin of the fenestra ovalis housing the head of the stapes. The otic capsule generally appears to have ossified from two centers, the prootic and opisthotic bones. In described anthracosaurs the two bones are suturally separate. In well-ossified temnospondyl genera, the two are usually solidly fused, without sign of suture; in poorly ossified types the two elements may be found as distinct entities. The prootic appears to have in general included the anterior part of the internal ear region and, laterally, the area above and anterior to the fenestra ovalis; the opisthotic primitively lay posterior to the fenestra ovalis and comprised most or all of the paroccipital process, including that area of the capsule visible in posterior view. Posteriorly the otic capsule was bounded by the metotic fissure, which is represented in the adult by the vagus foramen. In forms in which the opisthotic bone is well ossified, there are sometimes sutures dorsal or ventral to the vagus foramen which separate the opisthotic from the adjacent exoccipital. Ventrally the line of contact passes inward and forward to a tripartite meeting of opisthotic and exoccipital with basioccipital; dorsally the line of division passes upward to the ventro-median corner of the posttemporal fossa.

This situation persists, as far as known, in anthracosaurs. In advanced temnospondyls, however, the opisthotic becomes much reduced in degree of ossification; associated, apparently, with the need for an osseous framework in the general occipital region, the exoccipital takes over the ossification of the posterior aspect of the otic capsule and may extend far forward, upward and outward from the vagus foramen — upward to floor much of the posttemporal fossa, outward along the paroccipital process.

The posttemporal opening is a conspicuous feature of the occipital aspect of the capsule. It is essentially an excavation in the dorsal part of the paroccipital process. Primitively it is roofed by a thin osseous sheet, but this is absent in most cases, so that its apparent roof is formed by the adjacent dermal bones — tabular and postparietal. As seen posteriorly, its median wall is part of the area belonging in reptiles to the supraoccipital. However, this region is in temnospondyls occupied by the dorsal extension of the exoccipitals. In seymouriamorphs this area is little ossified; the cartilage which was presumably present is sheathed and functionally replaced by a stout descending flange of the postparietal.

The floor of the posttemporal fossa is formed by that part of the paroccipital process which is visible posteriorly as a bar-like structure. Primitively the greater extent of the bar ossifies as a portion of the opisthotic. When opisthotic ossification is reduced in advanced temnospondyls, most of the bar ossifies from the exoccipital center. The distal end of the bar has a different history. Even in some primitive types it appears that the opisthotic ossification fails to extend to this very peripheral region. An area here may be persistently cartilaginous. However, there appears to have occurred here at an early date an unusual process — the invasion of a cartilage by a dermal bone. The tabular tends to extend downward into the tip of the paroccipital process and form an endochondral ossification in that region. In primitive temnospondyls and anthracosaurs this region is limited in extent (it may be still preserved even in such reptiles as the pelycosaurs (Romer and Price 1940, pp. 203–204); in advanced temnospondyls the tabular ossification may extend well medially along the process to form a firm union with the advancing exoccipital.

The posttemporal opening is frequently regarded as a fenestra, a "window" without any degree of depth; actually, however, it may be seen in well-ossified material that it is a deep pocket, and is more properly termed the posttemporal fossa. It may have — like a similar structure in fishes, the fossa Bridgei — housed the origin of a part of the neck musculature (Säve-Söderbergh 1936; Romer 1941). The anterior border of this pocket may remain unossified. It appears to have been closed in life by a wall of either cartilage or bone; but there is a channel, perhaps best termed the posttemporal foramen, which runs forward dorsally to open onto the anterior face of the otic capsule lateral to the region of the trigeminal opening.

The fenestra ovalis is present on the lateral surface of the capsule. It is variable in size and, apparently, in construction, and it is un-

fortunate that our knowledge concerning it is far from complete. The opening should in theory be completely surrounded by otic capsule components, and this is presumably the case generally if not universally. In such a seymouriamorphan as *Kotlassia*, prootic and opisthotic definitely form the entire circumference. In temnospondyls, however, the tendency for reduction of ossification of these two elements results in the seeming entrance of other elements into the periphery of the opening; these include the parasphenoid, basioccipital and exoccipital. It is reasonable to conclude that there was in life a completion of the margins of the fenestra by cartilage proper to the otic capsule, but further data are needed.

In known temnospondyls the fenestra ovalis is non-projecting and low down along the ventro-lateral wall of the capsule. Little is known of the structure in embolomeres. Watson cites evidence that in one case the fenestral depression may have been persistently imperforate. In seymouriamorphs the opening is situated at the summit of a marked dorso-lateral outgrowth of the otic capsule.

In the discussion above of the paroccipital process only the occipital aspect was considered. The process, however, has considerable depth antero-posteriorly; its medial base extends forward dorsally to the anterior end of the capsule region in the neighborhood of the trigeminal nerve exit. The anterior surface of the process may be expanded lateral to the trigeminal opening, causing the development of a depression or pocket about this nerve opening comparable in certain regards to the piscine trigemino-facialis chamber. Lateral to this pocket, and at a higher level, may be found the anterior opening of the foramen leading forward from the posttemporal fossa; lateral again to this there may be an elevation or marking of some sort indicative of the attachment of the palatoquadrate complex (crista parotica); both pterygoid and epipterygoid may articulate with this parotic crest. Along this anterior face of the capsule, below and behind the trigeminal opening, there opens the foramen carrying back the main stem of the facial nerve; the course of the palatine ramus is seldom observed and may have been variable.

In well ossified primitive temnospondyls the anterior boundary of the otic region is difficult to delimit externally; with reduction of ossification it may be approximately determined as passing downward through the trigeminal opening and thence ventrally and somewhat posteriorly along a course between the fenestra ovalis posteriorly and the basipterygoid process anteriorly.

Both prootic and opisthotic were well ossified primitively and a

high degree of ossification persists in seymouriamorphs, as well as embolomeres and in certain early Permian temnospondyls. In later temnospondyls, however, the two elements may be greatly reduced. We have noted that exoccipital and tabular tend to take over the "duty" of ossification of the posterior face of the capsule. The remainder in many cases appears to have been nearly or entirely cartilaginous, although with relatively small and seemingly variable "nubbins" representing the two otic elements. The opisthotic appears to have had its center postero-dorsal to the fenestra ovalis; the prootic antero-dorsal to this opening. The latter is the better developed of the two elements in forms with reduced ossification.

The basisphenoid ossification has its center posterior to the area of the pituitary fossa in the floor of the braincase. In well-ossified primitive types the basisphenoid is in unbroken continuity externally with the otic region posteriorly and the sphenethmoid anteriorly and dorsally, and its boundaries can only be readily defined in forms in which endochondral ossification is reduced. The basisphenoid forms the floor of the endocranial cavity in the general diencephalic region; above, it continues in early temnospondyls into the orbital plate or laterosphenoid region which forms more dorsally the side walls of this part of the braincase. The floor of the braincase exhibits a depression containing the pituitary; this may take the form of a deep fossa (presumably a primitive feature), or a shallower structure (more comparable to that of modern amphibians). Anterior or lateral to the sella, the basisphenoid is pierced by foramina for the carotid arteries; the internal course of the carotid appears to have been variable, but is known in only a few cases. Internally there is sometimes seen a fissure anterior to this region separating the basisphenoid from the ventral part of the sphenethmoid anterior to it.

Posterior to the pituitary fossa, the basisphenoid is pierced by a transverse canal presumably transmitting, as in fishes, an interorbital vein. This is sometimes a small structure, carrying nothing but the vein itself. It may, however, become considerably enlarged and, somewhat after the fashion of actinopterygians, may have afforded a point of origin for part of the rectus eye musculature. This possibility was noted by Sawin (1941, p. 436) in the case of *Eryops*, and later by Säve-Söderbergh (1944) in the case of an unnamed Triassic amphibian. As figured by Watson (1926, figs. 12, 18), this area was in embolomeres an open fenestra from one surface of the braincase to the other. The sixth cranial nerve appears to have emerged from the braincase near the mouth of this canal.

Postero-laterally, the basisphenoid region bears on either side the laterally projecting basipterygoid process by means of which articulation with the palatal structures is effected. This process is bounded ventrally and posteriorly by the ensheathing parasphenoid. As noted in the discussion of the palate, this articulation was originally a freely movable one, and remains so in anthracosaurs and various early temnospondyls; the projecting process of the basisphenoid was received in a socket, a "conical recess", formed by epipterygoid and pterygoid. In later temnospondyls the articulation becomes a firm one; the underlying parasphenoid fuses with the pterygoid and in many cases this region of the basisphenoid fails to ossify. Even so, the form of this persistent articular process can be readily restored from the contours of the "conical recess". Above the process a ridge may continue upward along the surface posterior to the recess for the interorbital vein. Laterally the basisphenoid passes back smoothly and without evidence of suture in primitive forms into the lateral wall of the otic capsule behind the basipterygoid process, and ventrally the basisphenoid is covered completely by the parasphenoid. Internally, however, a definite posterior boundary to the basisphenoid is seen in well-ossified primitive forms; at about the level of the posterior end of the basipterygoid process, ossification ceases in the floor of the braincase, and a deep fissure, presumably filled with cartilage in life, separates the posterior end of the basisphenoid from the paired otic capsules and the basioccipital behind them. This fissure is reminiscent of the separation into two parts of the crossopterygian braincase at a similar position.

The basisphenoid appears to have been fairly well ossified in anthracosaurs, but in seymouriamorphs it tends to become more distinct through reduction of the orbital plate above it, and of the osseous floor of the braincase in this region. In advanced temnospondyls the basisphenoid becomes strongly reduced; it may become restricted to a small ossification in the neighborhood of the hypophysis, and even this appears to be absent in some cases.

The most anterior portion of the ossified braincase is the sphenethmoid region. In primitive, well-ossified braincases the sphenethmoid is fused without trace of suture to the basisphenoid and otic elements and hence is difficult to delimit. It perhaps includes posteriorly the general area here termed the orbital plate ("laterosphenoid"): the area of the lateral wall of the braincase anterior to the trigeminal recess and above the basipterygoid process of the basisphenoid, and running forward to the neighborhood of the optic

foramen. This plate is in general relatively thin, and liable to damage or loss in preservation or recovery. Apart from the optic foramen, it may be pierced by foramina for eye muscle nerves and blood vessels. In the few forms in which details are known, this area is not roofed. It appears to have enclosed the anterior part of the brainstem. Ventrally the walls of the orbital plate continue without break, in primitive forms, downward into the basisphenoid region.

In the more advanced temnospondyls the laterosphenoid area tends to lose its ossified nature to a variable degree, but was presumably continuous in cartilaginous form. In anthracosaurs, however, a different situation exists. A large open area is found here in embolomeres, running forward from the region of the trigeminus exit. This area was presumably here a definite opening in the cranial wall, as in living reptiles. It represents the opening which in the embryo lies between the otic capsule posteriorly and the pila antotica anteriorly and antero-ventrally. In embolomeres, as far as known, this opening is relatively small; in seymouriamorphs it is enlarged, because the anterior margin of the otic capsule is diagonally placed, sloping far backward dorsally.

The main portion of the sphenethmoid, lying forward of the region of the optic foramen, occupies the whole height of the braincase. In section the sphenethmoid is here V-shaped; in primitive forms, the V is a narrow one, with nearly vertical sides; in advanced temnospondyls, with a more platybasic type of skull, the element is broader and flatter. In well-ossified forms the ventral part of the sphenethmoid is a solid structure, sheathed ventrally by the cultriform process of the parasphenoid. More dorsally, the posterior portion may exhibit a single chamber which in life presumably contained the cerebral hemispheres and olfactory bulbs. Anteriorly there are paired tubular channels for the olfactory nerves (subdivided in *Eryops* into vomeronasal and proper olfactory components). In some forms in which the degree of ossification is not great, the interior of the bone remained cartilaginous, and the sphenethmoid consists merely of the perichondral ossifications forming the two branches of the V. Anteriorly the sphenethmoid expands in width in the direction of the nasal capsules of either side. The anterior end presents an unfinished bone surface in even the best ossified forms; from this surface the sphenethmoid was presumably continued forward in cartilage to the nasal structures. The extent of ossification of the sphenethmoid may be restricted anteriorly as well as posteriorly in advanced temnospondyls; in some instances, particularly in Triassic genera, the sphenethmoid

is unreported and may have become purely cartilaginous in nature.

The nasal capsules are not ossified in the slightest in any known labyrinthodont — a feature in which these forms show a reduction of ossification as compared with typical crossopterygians. In several instances in which the inner aspect of the roofing bones has been observed, markings in the nasal region have given suggestions as to the contours of these structures.

LOWER JAW

(Figs. 9, 10)

The general morphology of the lower jaw has been recently reviewed by Nilsson (1944). The length of the jaw ramus varies, of course, proportionately with head length and with the position of the glenoid articulation. The ramus tends to be subcircular in section anteriorly, deeper and relatively narrower posteriorly. In life the plane in which the jaw ramus lies appears to have tilted inward ventrally.

The outer jaw surface is sculptured, usually in a fashion similar to that of the skull roof. A lateral line groove may enter this surface near its postero-dorsal margin and descend parallel to the posterior margin (mandibular sulcus). In seemingly primitive forms this groove turns forward along the lower margin of the lateral surface; in advanced temnospondyls this sulcus is no longer present ventrally, and the lateral line either followed the ventral rim of the jaw or ran forward in the skin beneath the jaw rim. In many temnospondyls a more prominent groove is the sulcus dentalis or oralis which runs forward at a more dorsal level; there may be a short accessory sulcus above this last.

The two jaw rami are connected by a symphysis with interlocking denticulations on the dentary and splenial elements. The lower margin of the jaw ramus is usually somewhat rounded anteriorly, more sharply angulate posteriorly. The ventral margin curves sharply dorsally beyond the "angular" region which marks the deepest point of the ramus.

Dorsally, the jaw carries, in its anterior and middle portions, a flattened area occupied by the teeth and alveoli of the marginal tooth row; the outer wall of this alveolar area is higher than the inner. Often a pair of tusks, variably developed, is present near the symphysis internal to the marginal tooth row, and sometimes additional small teeth as well; symphysial tusks are unknown, however, in anthra-

cosaurs and brachyopoids. The coronoids may bear teeth of small size; they are more common at the posterior end of the coronoid series.

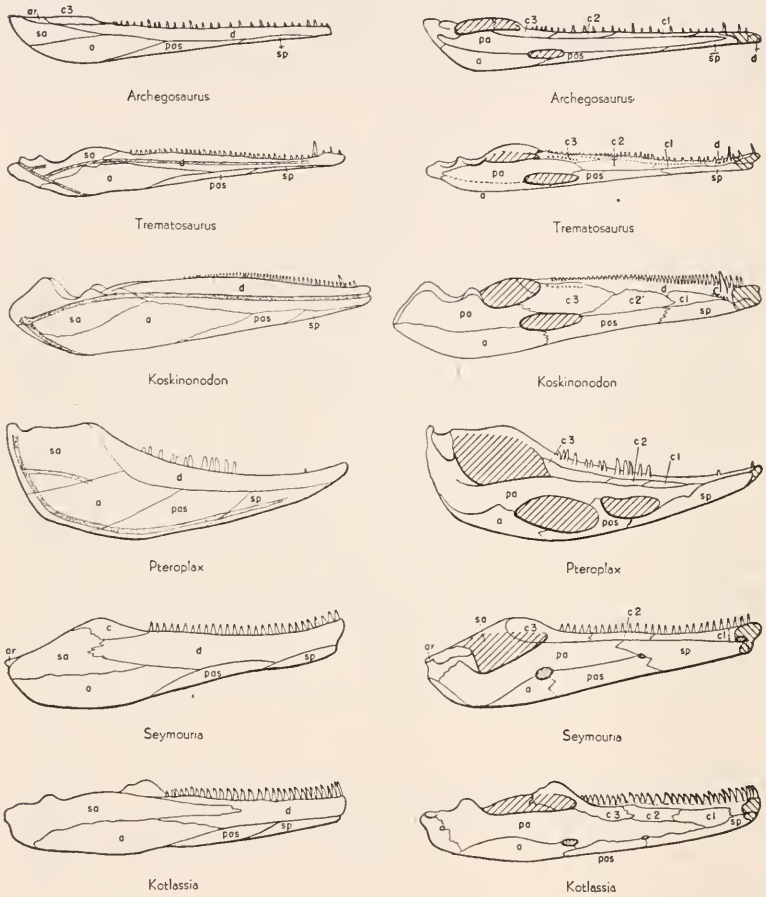

Fig. 9. Lower jaws. *Left*, external views of right ramus. *Right*, internal views of left ramus. *Archegosaurus* after Jaekel, Whittard; *Trematosaurus* after Jaekel; *Koskinonodon* after Branson and Mehl; *Pteroplax* after Watson; *Seymouria* after White; *Kotlassia* after Bystrow.

Exceptionally, a shagreen of teeth, analogous to that developed above on the dentary, may be present on the prearticular.

Posteriorly the dorsal surface bears the glenoid fossa for articulation with the quadrate. Anterior to the glenoid there opens dorsally the large oval adductor fossa, serving for admission of temporal muscula-

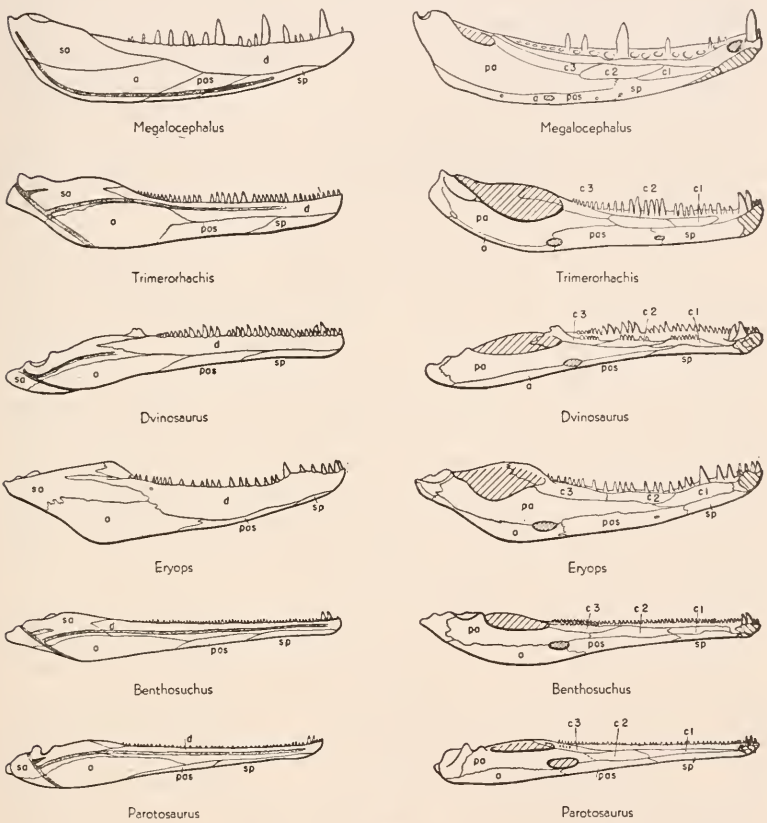

Fig. 10. Lower jaws (continued). *Megalocephalus* after Watson; *Trimerorhachis* after Case; *Dvinosaurus* after Bystrow; *Eryops* after Sawin; *Benthosuchus* after Bystrow; *Parotosaurus* composite.

ture, vessels and nerves. The medial wall of the fossa is usually much lower than the lateral, where there tends to form a "coronoid" process of one type or another. Posterior to the glenoid fossa there develops in many advanced groups a pronounced retroarticular process for the musculature opening the jaw.

Medial to the glenoid fossa a foramen entering the adductor fossa transmits the chorda tympani nerve. Farther forward and more ventrally situated on the inner surface of the jaw is a meckelian foramen or fenestra, often of large size. Usually a second foramen of the same sort is present more anteriorly; this is typically smaller, or may be subdivided into several small openings. Running forward internally from the adductor fossa is an elongate canal surrounded by dermal bones. This has been variously named; it is reasonably termed by Nilsson the meckelian space, since it may have been occupied in great measure in life by the meckelian cartilage as well as by nerves and blood vessels supplying the anterior part of the jaw ramus.

The pattern of bony elements is extremely uniform in labyrinthodonts. Nine dermal bones are present in all adequately known genera. Largest of these is the dentary. This occupies much of the outer surface of the anterior part of the jaw, bounded below by the splenial elements, which it overlaps, posteriorly by angular and surangular. Frequently a slender posterior prolongation of the dentary overlaps the surangular; postero-dorsally the dentary is bounded by the posterior coronoid. The narrow dorsal surface of the dentary forms an elongate groove, in which are found the series of alveoli for the marginal teeth. Beneath this region the dentary forms the roof and part of the lateral wall of the meckelian canal. There is little medial exposure of the dentary below the tooth row. Anteriorly the dentary forms the major part of the symphysis.

Below and behind the dentary on the outer surface of the jaws is a series of four elements comparable to the infradentaries of crossopterygians; the sutures between successive elements almost uniformly slant downward and backward in roughly parallel fashion. The two anterior elements, the smallest of the series, are comparable in a broad way to the single splenial of reptiles. Their lateral exposure is in general reduced in post-Carboniferous types, to the profit of the dentary. Of the two, the more anterior, which takes part in the symphysis, is generally regarded as the true homologue of the reptilian splenial, but the question is perhaps an open one (cf. Nilsson, 1944, pp. 42–47). The two splenials generally have a modest exposure on the inner surface; they are usually bounded dorsally, from back to front, by prearticular, the coronoid series, and (far anteriorly) the dentary. They form the floor of the meckelian space. The posterior splenial usually enters the anterior margin of the posterior meckelian fenestra; an anterior meckelian fenestra, when present, usually lies within the confines of the posterior splenial.

The angular occupies a large area on the outer surface of the jaw, centered on the "angular" region of the lower margin; it is bounded antero-ventrally by the posterior splenial, antero-dorsally by the dentary, and dorsally by the surangular. It occupies a relatively narrow ventral strip of the inner surface, running back from the region of the posterior meckelian fenestra and bounded above by the prearticular.

The surangular occupies the upper outer surface at the posterior end of the ramus. Its dorsal margin forms much of the lateral border of the adductor fossa. The surangular tends to fuse with the articular, and in great measure ensheathes that element, wrapping about its posterior surface to the inner aspect of the jaw, where it gains contact with the prearticular, and also buttressing it antero-laterally. The retroarticular process, when developed, is formed by the surangular.

On the inner surface, below the dentary, there is present a longitudinal series of three relatively long and narrow elements, sometimes tooth-bearing, which are comparable in many ways to the three lateral elements of the palatal group in the upper jaw (Romer 1940a). These are the coronoids, sometimes identified merely by number, sometimes individualized by distinct prefixes. The posterior coronoid, generally believed homologous with the single element retained in most reptiles, forms the anterior rim of the adductor fossa and, extending back along the lateral wall of that opening, tends to rise upward to form (with the aid of the surangular) a "coronoid process" to which the more lateral portions of the jaw musculature presumably attached.

A variable — but generally large — area of the inner surface of the jaw is occupied by the prearticular. One gains the impression that ontogenetically it is late in development, and completes the jaw surface by filling in, in an obliging fashion, any areas not occupied by its dermal neighbors. Posteriorly it is widely expanded, and extends from the median margin of the adductor fossa downward nearly to the ventral margin of the ramus, where it is bounded by the angular. It may fuse with the articular, which it sheathes medially. Anteriorly it narrows between the coronoids dorsally and the posterior splenial ventrally. In most cases it extends no farther forward than a point below the posterior part of the middle coronoid, but exceptionally may extend much farther toward the symphysial region. In general the anterior extension is greater in anthracosauroids. Exceptionally, a shagreen of teeth has been reported on the prearticular (comparable to the pterygoid dentition of the palate). Internally the prearticular forms much of the median wall of the meckelian space.

The articular is in general the only endoskeletal element present in the lower jaw. As typically developed, it forms a compact block of bone at the posterior end of the jaw ramus. It is exposed dorsally, where it bears a depressed area, usually subdivided in two by a ridge, for the reception of the quadrate condylar surfaces. Anteriorly it forms most of the posterior wall of the adductor fossa. On all other surfaces it is sheathed by surangular and prearticular elements with which, as noted, it is usually indistinguishably fused.

In life there probably extended forward from the articular a meckelian cartilage, lying in the floor of the adductor fossa and extending forward in the meckelian space. In some instances the articular is seen to continue forward as an ossification along this cartilage. In various other vertebrates ossification may occur more anteriorly in this cartilage; among labyrinthodonts such ossifications have been observed only in two trematosaurs (Nilsson 1943, pp. 17 ff.).

VISCERAL ARCH STRUCTURES

The stapes is known in a considerable number of forms from the Permian and Triassic; we know little, however, of its history in earlier times. It usually takes the form of a rod, generally elongate, extending from the fenestra ovalis outward and upward toward the otic notch and the presumed position of the tympanic membrane. The distal end of the stapes was cartilaginous; one may assume that beyond this point there may have been processes connecting with the quadrate region or the hyoid apparatus, but there is no direct proof, although appropriate processes or depressions for its articulation are sometimes seen on the quadrate. The shaft may have a slight elevation or ridge which was connected with the under surface of the paroccipital process. This is equivalent to the dorsal process known in early reptiles on the one hand, and crossopterygians on the other. But no known labyrinthodont exhibits the well developed divergent process found in both these types, and the problem of the evolution of stapedial form (associated intimately with that of evolution and position of the tympanum) is one far from solved. The stapes is as yet unknown in embolomeres. In seymouriamorphs, owing to the unusual conformation of the otic region, the stapes is very short but unbranched and not at all reptilian in type.

Every well preserved and well ossified stapes exhibits a stapedial foramen of tetrapod type near the base. The base is expanded to

form a footplate for insertion into the fenestra ovalis; in some instances an accessory process at the base appears to have been in continuity, by perichondral ossification, with the otic capsule at the anterior margin of the fenestra.

Undoubtedly, as in both major orders of living amphibians, the larval labyrinthodont possessed a complex and highly developed branchial skeleton, which was, for more terrestrial types, reduced with growth and metamorphosis, but was retained in paedogenetic genera. Unfortunately it would appear that in most cases the branchial skeleton was persistently cartilaginous; and even if ossified, these small and loosely articulated structures would tend to be lost before burial or subsequently lost from the fossil specimen. In consequence our knowledge of the gill skeleton is meagre; it is best known in the neotenous genus *Dvinosaurus* (Bystrow 1938).

AXIAL SKELETON

(Figs. 11, 12)

In relatively few amphibians is the vertebral count adequately known. Regional differentiation is difficult because of the fact that primitively, and apparently generally, all vertebrae, to and including the proximal caudals, were rib-bearing. Watson (1926, p. 232) has offered evidence indicating that in at least one embolomere there was no specialized sacral rib, but that pelvic support was distributed over a number of segments. This may reasonably be interpreted as a truly primitive condition, but in most labyrinthodonts a distinct sacrum is evident, and presacral (trunk) and postsacral (caudal) series may be established. The presacral count is frequently close to 24 segments, and one may reasonably assume that this is a primitive number. Variations, however, certainly occurred; some embolomeres, for example, had 35 to 40 presacrals.

Analogous to the complexities seen in the atlas-axis structure of amniotes, we find considerable variation in the structure of the most anterior vertebrae in labyrinthodonts. In a primitive rhachitome the intercentrum and paired neural arches of the first cervical form a circular articular area which met the margins of the single circular occipital condyle; the seymouriamorphs and, I suspect, the embolomeres retained this condition. In later temnospondyls, however, considerable modification of the structure occurred in correlation with subdivision of the condyle. There tends to occur a broadened

atlas in which intercentrum and neural arches are fused; this bears a pair of large subcircular facets anteriorly for the skull condyles. A small proatlas is known in certain instances, and may have been frequently, if not universally, present in primitive forms.

In general there was but a single sacral vertebra; in a few forms, however — dissorophids, seymouriamorphans — a second segment

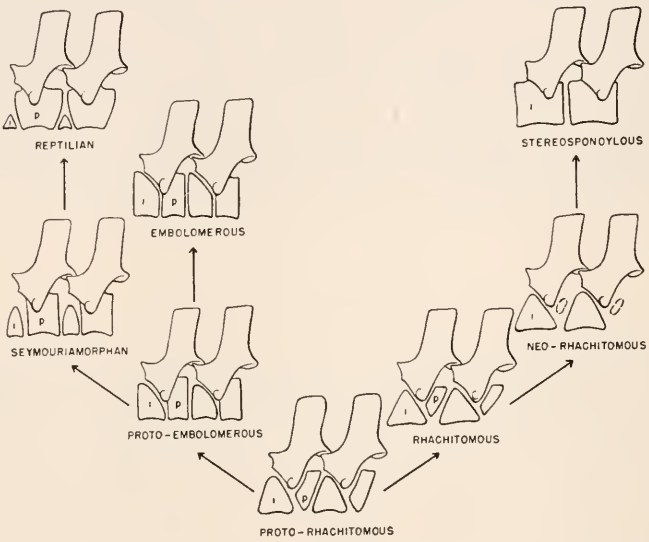

Fig. 11. Diagram to show phylogenetic arrangement of vertebral types as here advocated. *i*, intercentrum; *p*, pleurocentrum (true centrum). Two segments, viewed from left side.

may take on an accessory sacral function. In but few cases is the tail anywhere nearly completely known. It seems certain, however, that it was primitively elongate and that it remained so in most cases.

The neural arch, obviously preformed in cartilage, is generally surmounted by a neural spine. The length of the spine is variable, a tendency for relative elongation being apparently associated with increase in absolute size of the animal. The spine is often somewhat expanded at its tip, where it presumably was embedded in the dermis of the animal. This tip may be sculptured after the fashion of cranial dermal bones, a feature indicative of its superficial position. This sculpturing presumably indicates an area of dermal ossification which

may be fused to the neural arch proper or may persist as a separate dermal element. In dissorophids the sculptured spines are of normal length; in Permian zatrachydids the spines are exceptional in a tendency to great elongation, comparable to that of pelycosaurs. In many instances — in part due to individual immaturity — the spines are unfinished dorsally, a condition indicative of a cartilaginous continuation of the spine in life. In a few small forms there are no indications of any degree of spine development above the rounded contour of the neural arch.

In general the pairs of anterior or posterior zygapophyses are situated close together with the plane of the articular surfaces tilted upward laterally from the horizontal, and with the dorsal contours of the neural arches above the posterior zygapophyses concave in end view. In the Seymouriamorpha, however, the neural arches are similar to those of reptiles, with the members of each pair of zygapophyses widely separated and with horizontal surfaces, and the arch contours are convex and "swollen". On each side, the pedicel of the arch bears, in all rib-bearing segments, a diapophysial lateral process or facet for the rib tubercle. In general the pedicel is V-shaped below in lateral view, with broad anterior and posterior surfaces apposed to the vertebral centra. In few instances, however, are the arches fused with centra.

The Labyrinthodontia are apsidospondylous — *i.e.*, appear to have centra developed primarily from cartilaginous arcualia (although much of the growth may well be perichondral in nature). There is (except for a report in *Archegosaurus* which demands re-investigation) no evidence of more than two types of arcualia in a segment — anteriorly an intercentrum (never, as far as known, paired), posteriorly a structure or structures apparently corresponding to the true centrum of amniotes but often represented by a pair of lateral ossifications.

The intercentrum is characteristically (in forms as far apart as the seymouriamorphs and typical rhachitomes) a half ring, centered ventrally and extending upward part way around the curve of the column on either side. It may ossify only superficially as a thin perichondral shell, or may be considerably thickened, leaving, however, a space in the center of the column for the persistent notochord. In side view the intercentrum, when in this typical condition, is wedge-shaped, with the apex dorsally (between successive pleurocentra). Typically a subcircular unfinished area is present along the posterior margin for the attachment of the capitulum of the rib; this sometimes develops into a low, laterally projecting articular process.

In several diverse groups, the intercentrum becomes a complete or nearly complete ring. In the embolomeres it becomes a complete if short cylinder, pierced centrally for the notochord and somewhat convex on both anterior and posterior faces. This type of intercentrum is thin and usually not well ossified dorsally, indicating its derivation from the typical crescent. In certain Triassic temnospondyls (*Cyclotosaurus*, metoposaurs) a similar structure may develop in parallel fashion; here, however, the ring is either incomplete dorsally, exhibiting a V-shaped nick in which the notochord is enclosed, or is a complete ring with a notochordal perforation eccentrically placed toward the upper margin; the element has apparently found it difficult (so to speak) to encircle the notochord. Even among seemingly typical rhachitomes, a comparable development is seen in *Trematops* and *Parioxys*. Still another variant is that discussed under the plagiosaurs. There one finds a rather elongate cylindrical "centrum" similar in general regards to that of lepospondyls but presumably a much modified intercentrum; the notochordal canal has disappeared.

We have described above the ossified intercentrum. In life, the cartilaginous intercentrum may have been considerably larger in many cases than the ossification occurring in and about this cartilage. In *Eryops*, for example, the area which could have been occupied in life by the intercentrum extended well dorsally and may have surrounded the notochord. Thus the repeated development of an ossified ring-intercentrum does not necessarily imply any expansion of the intercentral structure, but merely implies better ossification.

In some Crossopterygii the intercentrum is described as a pair of laterally placed half-rings. Similar structures have been reported in certain early temnospondyls, but the evidence does not seem too definite.

The pleurocentrum is equally variable in its development. In typical rhachitomes the ossified pleurocentrum is a paired structure. Each member of a pair is a diamond-shaped structure lying well dorsally below and behind the pedicel of its proper arch. Its upper end is interposed between two successive arch pedicels; its ventral end is often pointed and elongate, extending downward between successive intercentra. Internally the degree of ossification appears to be variable, but conditions here are seldom observed. In well ossified specimens of *Eryops* and *Trimerorhachis* the pair of pleurocentra may fuse with one another above the notochord and below the neural canal. Such a structure is analogous to that of the intercentrum ventrally. It is probable that a cartilaginous connection

between paired ossification centers may have been present in other cases.

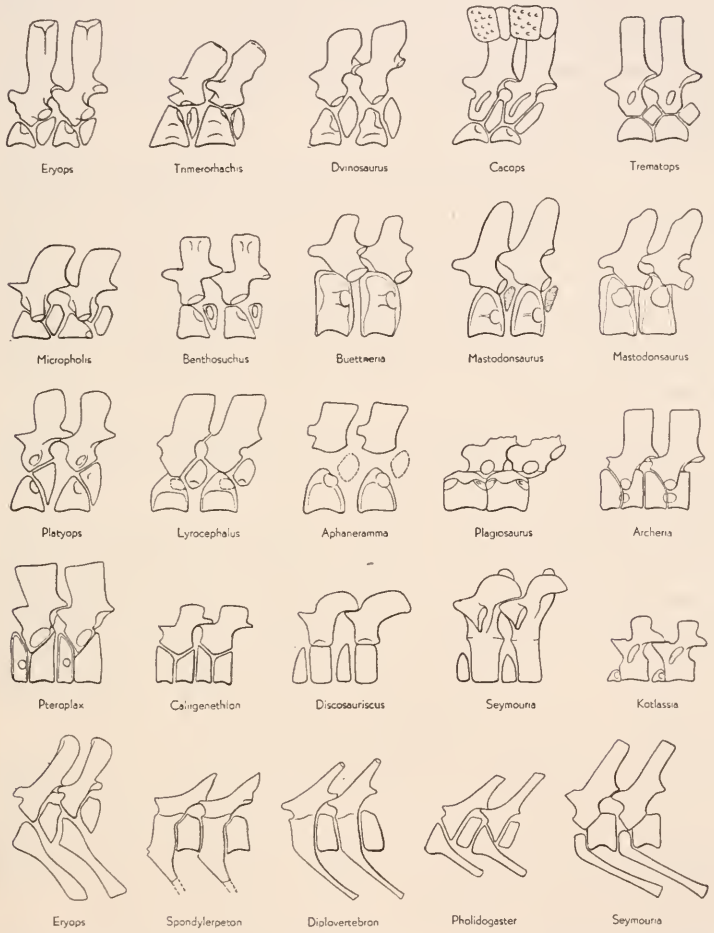

Fig. 12. Two vertebrae, viewed from left side, of various labyrinthodonts. First four rows, dorsal vertebrae; lower row, caudals. Diagrammatic. *Trimerorhachis* after Case; *Dvinosaurus, Benthosuchus, Kotlassia* after Bystrow; *Cacops, Trematops, Archeria* after Williston; *Micropholis, Pteroplax, Pholidogaster* after Watson; *Mastodonsaurus, Lyrocephalus, Aphaneramma* after Nilsson; *Platyops* after Bystrow and Efremov; *Calligenethlon* after Steen; *Discosauriscus* after Credner; *Seymouria* after White; *Diplovertebron* after Fritsch.

In the more advanced temnospondyls the pleurocentrum becomes reduced in degree of ossification and area occupied. Ossification may cease entirely, although a gap, surely filled by a cartilaginous pleurocentrum, usually persists. In Triassic brachyopoids there appears to have been complete loss of these structures; little or no area remains for the accommodation of a pleurocentrum between successive intercentral elements.

In the Anthracosauria, on the other hand, the pleurocentrum is the major element of centrum construction. In both embolomeres and seymouriamorphs it is a ring complete ventrally as well as dorsally, longer antero-posteriorly than the intercentrum, pierced centrally for the notochord and concave both anteriorly and posteriorly.[1] This is essentially the reptilian condition; there is no evidence of any arch element in this ring other than the pleurocentrum, and hence this amphibian structure is the equivalent of the true centrum of amniotes.

The three classic types of vertebrae among labyrinthodonts are the embolomerous, rhachitomous and stereospondylous to which, with the inclusion of the seymouriamorphs, we may add the proreptilian type found in that group.

The embolomerous type is that in which both intercentrum and true centrum (pleurocentrum) form complete rings. Watson reasonably argued that this was, in all probability, the primitive labyrinthodont condition. The Embolomeri, in which such vertebrae are present, are very primitive amphibians; this type of vertebra is common in Carboniferous rocks; until recently no other type of vertebrae was known from typical Carboniferous deposits, and no other group of labyrinthodonts of comparable age was known.

From the embolomere vertebra that of the seymouriamorphs and reptiles may be readily derived by a reduction of the intercentrum to a wedge. The rhachitomous type may be theoretically attained by a loss of the dorsal half of the intercentrum and a still greater reduction of the true, pleural, centrum so that the ventral portion is lost and the dorsal half further reduced to paired nubbins.

In the typical rhachitomous vertebrae the intercentrum is a ventral wedge-shaped hemicylinder; the pleurocentrum a pair of lozenge-shaped dorsal structures fitting between successive intercentra and arch pedicels. This was at one time thought primitive; and currently,

[1]Nilsson (1943a, p. 249, footnote) objects on theoretical grounds to the statement that in embolomeres both intercentrum and pleurocentrum are biconcave. However, the embolomeres were unacquainted with theories and (as any example of "*Cricotus*" shows) stubbornly exhibit a double amphicoelous condition.

mounting evidence suggests that this is actually the case, despite the favor recently shown the embolomerous hypothesis.

Only a moderate percentage of Carboniferous types have any real claim to inclusion in the Embolomeri. Very few are known definitely to have possessed embolomerous structure. Some Carboniferous amphibians are definitely known to possess rhachitomous vertebrae and many may be reasonably assumed to have possessed them. Certain of these forms appear to have been as primitive as the embolomeres in other structural features. All these facts indicate that the rhachitomous type of vertebra has as strong a claim as the embolomerous to a primitive position in labyrinthodont evolution; this thesis is here accepted as a reasonable working hypothesis.

It is simpler, and seemingly more natural, to explain vertebral evolution among the labyrinthodonts if the rhachitomous type be considered as basic. Although double-disc centra are found among the fishes, the crossopterygian vertebrae, as far as known, are never embolomerous. The intercentra in crossopterygians are usually well developed in an apparently variable fashion; the pleurocentra, on the other hand, as far as known, are never more than small, dorsally situated paired structures (cf. Gregory, Rockwell and Evans 1939). They were thus closer to the rhachitomous structure, and relatively little was needed to convert them into the type seen in primitive temnospondyls. The reptilian structure was presumably attained by an expansion of the pleurocentrum; the embolomerous vertebra, on this theory, showed still further modification in the expansion of the intercentrum as well.

The hypothesis of vertebral evolution here adopted assumes that rhachitomous vertebrae were present in an array of primitive amphibians — as the ichthyostegids and loxommids — which are not rhachitomes in the classical sense; further, as will be noted, many of the forms usually placed in the Stereospondyli actually possessed rhachitomous vertebrae. I have here used Rhachitomi as a taxonomic term, but in a restricted sense, excluding both ichthyostegals and more advanced rhachitomous types, the latter being here included in the Suborder Stereospondyli despite the retention of a more primitive or transitional vertebral structure.

In some Triassic forms there has long been known a type of vertebra termed stereospondylous (because of its deceptive simplicity of structure). In this, the intercentrum alone is present, as a complete or nearly complete ring. It is agreed that this condition has been arrived at by reduction and loss of the pleurocentra and a concomitant

upward growth of the intercentrum. This evolutionary development furnishes further reason for belief in the acceptance of the rhachitomous rather than the embolomerous type as primitive; for under the first hypothesis the evolution of the stereospondylous condition is a simple, straightforward story; on the hypothesis that the embolomere condition is primitive, we are forced to the strained conclusion that the disc-shaped intercentrum of the embolomere was first reduced to a ventral wedge of the rhachitome type and that then, for no apparent reason, reversed its trend and reassumed its former condition. Reversals in evolution do occur; but they should not be assumed if other reasonable explanations are available.

It was once believed that the stereospondylous condition was practically universal among Triassic labyrinthodonts and these forms were consequently considered as forming an Order (or Suborder) Stereospondyli. It has, however, been apparent for several decades that the so-called Stereospondyli were more or less polyphyletic in origin; and we now know further that a considerable percentage of them did not possess stereospondylous vertebrae, but were in an essentially rhachitomous stage of evolutionary development. Despite this, I have for convenience retained the term Stereospondyli as a taxonomic unit to include the forms with actual stereospondylous vertebrae and in addition more primitive types which appear to be their common ancestors — the neorhachitomes.

Recent work, particularly that of Efremov and Bystrow, has revealed the presence in the late Permian and early Triassic of forms advanced over the typical rhachitomes in vertebral and other structures but not yet arrived at the general structural conditions seen in typical Triassic labyrinthodonts. These amphibians have been reasonably termed the Neorhachitomi or neorhachitomes. The word "neorhachitomous" has also been used as descriptive of vertebral structure. Current usage is loose, and the term may be applied (1) to forms in which the pleurocentra are still ossified, but the ossification is much reduced; or (2) to such forms plus others in which the pleurocentra were obviously present as cartilages, but unossified. In other sections we refer repeatedly to neorhachitomes as forms illustrative of an evolutionary stage between typical Permian temnospondyls and Triassic descendants, but use the term for a structural stage rather than a taxonomic unit, and without necessary implications as to the condition of the pleurocentra.

Central elements usually remain discrete from one another and from the neural arch; fusion, however, may occur in certain cases:

in old individuals or in restricted regions of the column. Evidence on this point is summarized by Bystrow and Efremov (1940, fig. 88, etc.). I doubt, however, whether, as suggested, such fusion has actually led to a definitive stereospondylous state.

Caudal chevrons, comparable to those of early reptiles, are found in all labyrinthodonts in which the tail is preserved. They are absent, as in reptiles, in the first few segments.

As noted above, ribs may be present on all segments from axis to proximal caudals. There is great variation in rib structure from group to group and in individual forms from region to region in the column; our information is, however, very sketchy in most cases.

The anterior cervical ribs are short; the length increases posteriorly so that the longest ribs are found in the dorsal region beneath and just posterior to the shoulder girdle; thence there is a gradual diminution in length toward the sacrum. Beyond this landmark, proximal caudal ribs may be of modest length, but there is a fairly sharp decrease to a point where the rib is a mere nubbin and finally disappears. The most anterior (cervical) ribs terminate in a "finished" tip, obviously not continued in cartilage, and the same condition holds for those in the posterior part of the trunk and in the tail. In the region of longest ribs, however, well preserved specimens may show an unfinished tip, presumably continued by cartilage and hence reasonably interpreted as possessing a sternal connection. This situation, common in amniotes, but not found in modern amphibians, tends to distinguish a thoracic region from a more anterior cervical and a more posterior lumbar region. As in many early reptiles there is a tendency for expansion of the ribs in the general "dorsal" region (and the posterior cervicals as well), a condition making for better attachment of serratus musculature. In some instances, at least, this expansion may take the form of posterior projections comparable to uncinate processes. As a study of *Eryops* specimens indicates, such expansions may show considerable variation even among individuals of the same species and hence may be unreliable for diagnostic purposes.

Typically the anterior vertebrae of early tetrapods have two points of attachment; a ventral capitular one on the posterior edge of the intercentrum and sometimes extending across onto the adjacent margin of the pleurocentrum, and a tubercular connection with the transverse process of the neural arch. Anteriorly these two areas are widely separated; posteriorly the capitular area tends to move upward toward the tip of the intercentrum or transfer itself

to the adjacent margin of the pleurocentrum; the tubercular attachment meanwhile descends toward the ventral edge of the arch pedicel, so that the "spread" of the combined articular areas is a small one. Correspondingly we find that on the proximal end of the rib, the distance between capitular and tubercular margins is great in the anterior ribs, and may gradually decrease posteriorly.

In most early reptiles capitulum and tuberculum are very distinct processes, particularly in the anterior part of the column. This condition holds in seymouriamorphans and, apparently, in embolomeres. In the rhachitomes, however, there is little apparent individuality of capitulum and tuberculum; there appears to be a continuous, undivided articular surface, a "holocephalous" condition. We may note, however, that the proximal end of the rib does not exhibit at any point a finished surface; it may have, in life, possessed a short cartilaginous proximal continuation in which discrete capitular and tubercular areas, separated by the customary notch for blood vessels, may have been present.

We have noted that in the most primitive amphibians there may have been no development of a typical sacral region. In most amphibians, however, there is a single highly developed sacral rib; in a few cases the next succeeding rib may touch the ilium and be considered as an accessory sacral. The sacral rib is short but very stout and terminates in a large flattened oval or leaf-shaped surface applied to the inner side of the iliac blade.

APPENDICULAR SKELETON

In many genera little or nothing is known (or described) of the girdles or limbs, and where known, descriptions are usually brief and non-comparative in nature. Appendicular structures are thus of relatively little use at the present time in studies on amphibian evolution; such a review as that of Nilsson (1939) on the cleithrum and humerus is indicative of the potential value of comparative studies in this regard. Because of the current lack of useful data, most of the appendicular structures will be but briefly described here.

In the dermal shoulder girdle (Figs. 13, 14) the labyrinthodonts almost universaly possessed three elements — paired cleithra and clavicles and a median ventral interclavicle. Watson (1926, pp. 232–234, fig. 25) has described a dermal girdle which he believed associated with the embolomere *Eogyrinus* in which the paired elements

were broad plates throughout their length; as noted elsewhere, however, this association may be questioned, and in all other cases the cleithrum and dorsal part of the clavicle are relatively slender structures. In this same instance the evidence suggests a connection of the cleithrum with the skull via a posttemporal element, as in fishes; in all other known cases, however, there is no evidence of such a connection although (as noted by Williston and later writers) the girdle lies close behind the skull, with little development of a discrete neck region.

The upper end of the cleithrum is generally curved backward and somewhat expanded to cap the top of the scapular blade; below this area the cleithrum descends the anterior margin of the scapula as a rod-like structure which articulates with the clavicle. The dorsal expansion may be absent, and the cleithrum (much as in some early reptiles) may be reduced to its rodlike portion. In plagiosaurs the cleithrum is broadened throughout, in piscine fashion.

The dorsal end of the clavicle typically articulates with the cleithrum well down the anterior margin of the scapula, at a point corresponding to the acromion of more highly developed amniotes, and usually continues downward from this point as a rod-like structure similar to the adjacent part of the cleithrum. In both plagiosaurs and metoposaurs the upper end of the clavicle is, exceptionally, expanded in variable fashion. As it progresses ventrally it lifts off from the surface of the dermal girdle and turns medially, following the contours of the body, onto the ventral surface; there it expands into a plate which articulates with the interclavicle. In more round-bodied types the curvature is gradual; in flat-bodied forms, a marked angulation is present, sharply setting off the dorsal spine-like section from a ventral plate. The ventral expansion is variable; in more terrestrial types, such as *Eryops* or *Cacops*, it is small and spoon-shaped; in depressed forms the clavicle may expand ventrally into a very large flattened triangular structure.

The interclavicle is most characteristically developed as a diamond-shaped ventral plate with one of its diagonals in the longitudinal axis, so that there are two margins facing either side of the body. On either side the clavicle overlaps the antero-lateral margin of the interclavicle to a variable degree; in many forms the two clavicles meet in the midline, or come close to one another, and may virtually conceal the two anterior quadrants of the interclavicle. As in the case of the clavicles, the size of the interclavicle varies greatly; it is generally small in more terrestrial types, expanded into a large flat

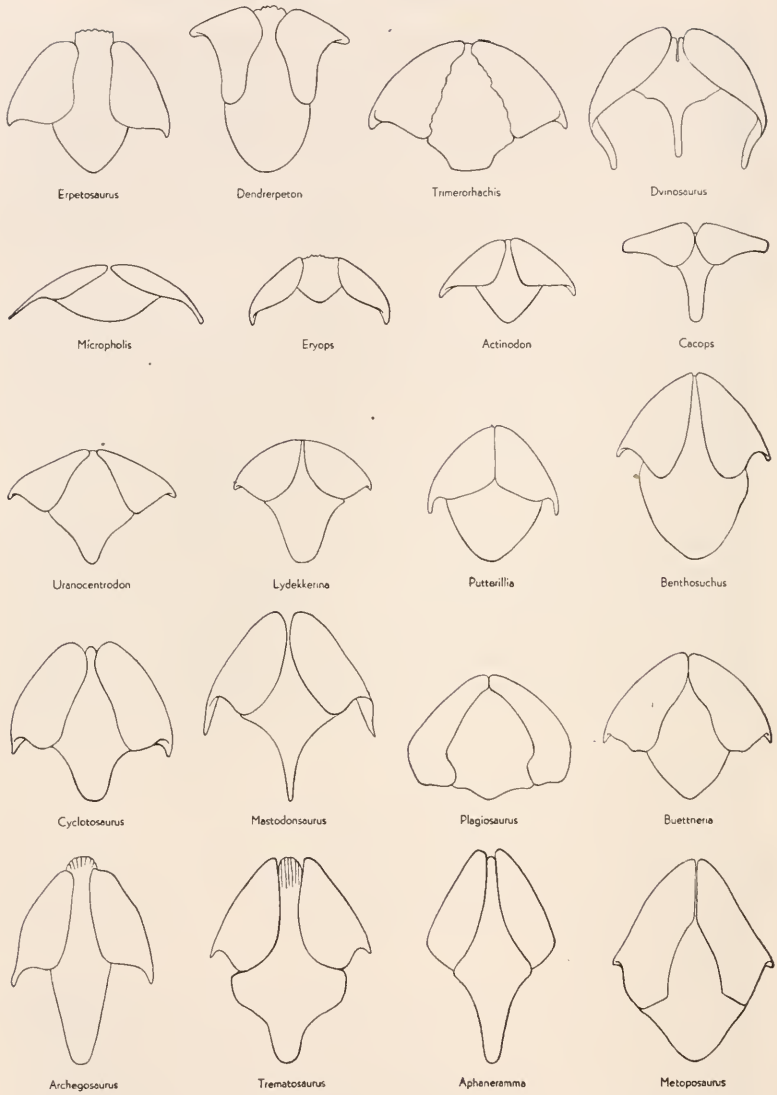

Fig. 13. Diagrams of dermal shoulder girdles (clavicles and interclavicle) of various temnospondyls, seen in ventral view. *Dendrerpeton*, after Steen; *Trimerorhachis*, *Buettneria* after Case; *Dvinosaurus*, *Benthosuchus* after Bystrow; *Micropholis*, *Lydekkerina* after Watson; *Actinodon* after Gaudry; *Cacops* after Williston; *Uranocentrodon*, *Putterillia* after Broom; *Cyclotosaurus*, *Mastodonsaurus*, *Metoposaurus* after Fraas; *Plagiosaurus* after Huene; *Archegosaurus* after Jaekel; *Trematosaurus* after Burmeister; *Aphaneramma* after Nilsson.

plate in aquatic and flat-bellied animals. Diagnostic to some extent is the shape of the posterior part of the interclavicle. A common temnospondyl type is that with two fairly straight margins converging to a blunt point; in others the posterior end is broadened and rounded to a variable degree. A posterior extension is rare in temnospondyls (but see *Cacops, Dvinosaurus, Mastodonsaurus*). In the anthracosaurs, however, a stem appears to develop, presumably in connection with the attachment of the pectoralis musculature. In embolomeres the

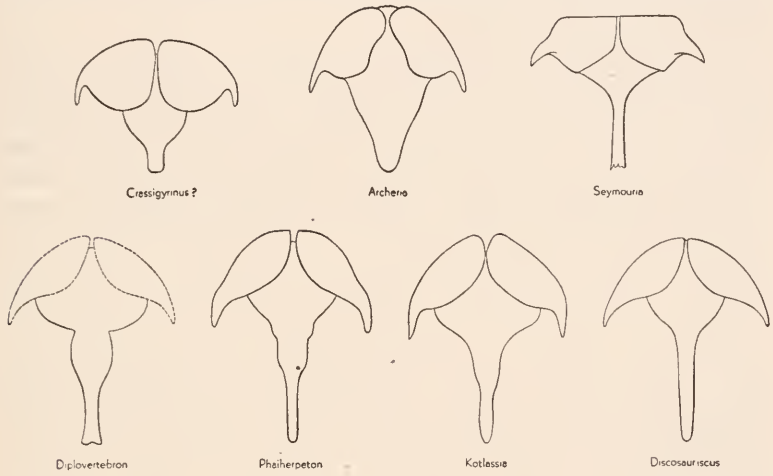

Fig. 14. Diagrams of dermal shoulder girdles of various anthracosaurs. *Crassigyrinus* (?) after Huxley; *Seymouria* after White; *Diplovertebron, Phaiherpeton* after Fritsch; *Kotlassia* after Bystrow; *Discosauriscus* after Credner.

stem, as far as known, is short; in seymouriamorphs it is an elongate structure, comparable to that in reptiles.

The anterior end of the interclavicle may be striate or pectinate, presumably in relation to the attachment of longitudinal throat muscles. The ventrally exposed surface of both interclavicle and clavicles usually bears an ornamentation comparable to that of the dermal skull elements.

In fishes the underlying "primary" — or better endochondral — girdle was small, and among amphibians the same is true of the supposed *Eogyrinus* girdle mentioned above. In all other cases, the girdle is much expanded, although in immature specimens, or genera in which ossification is reduced, much of the structure remained in a

cartilaginous condition. In most labyrinthodonts there is apparently but one ossification in the endochondral girdle, and there is evidence (Watson 1917) indicating that this element has its center of ossification situated dorsally, thus suggesting homology with the scapula of amniotes. In *Seymouria*, however, there is a second, ventral, ossification corresponding to the more anterior of the two coracoid ossifications of reptiles. The fact that the Anura (and *Diplocaulus*) possess a separate coracoid suggests that two ossifications may have been a more common condition in early amphibians than our present fossil evidence would suggest.

The morphology of the primitive tetrapod endochondral pectoral girdle, almost identically constructed in both early reptiles and early amphibians, has been described in detail by various writers, including Watson (1917), Romer (1922) and Miner (1925). The structure includes an elongate scapular blade placed nearly vertically within the flank of the animal, and a ventral coracoid plate turned inward below this region. Behind the lower end of the blade and above the posterior part of the coracoid plate was the elongate, screw-shaped glenoid cavity, buttressed by thickened bone areas above and internally. A coracoid (precoracoid, supracoracoid) foramen, presumably transmitting a nerve, as in many living tetrapods, pierced the anterior part of the coracoid plate. A glenoid foramen, unknown in living tetrapods and found in few if any reptiles, is sometimes reported below the glenoid region; White (1939, pp. 366-367) points out that such a structure may be confused with a nutrient foramen entering the bone at this point. A supraglenoid foramen is found within a triangle of bone forming a buttress above the anterior end of the glenoid region. This opening, not present, or at least not well developed, in any living tetrapod, appears to have been primitively of large size. Coracoid and glenoid foramina open internally into a large crescentic fossa which is a prominent landmark on the inner surface of the girdle.

No sternum has ever been reported, but it is generally assumed that some cartilaginous structure of this sort may have been present in life between the posterior margins of the two coracoid plates.

The pelvic girdle (cf. Romer 1922 etc.) appears to have consisted from the first of three elements — ilium, pubis and ischium, the three meeting in the acetabulum; in poorly ossified forms, however, the pubis (as in living amphibians) tends to remain in a cartilaginous condition.

The fish ancestor presumably lacked an iliac blade or process of

any sort, since this structure seems to have developed primarily in connection with the support of the girdle on the sacral region of the vertebral column. A primitive type of ilium, found in a few early amphibians, developed as a rod-like structure extending diagonally upward and backward from the acetabular region, and presumably connected along its course by ligaments with a series of "semi-sacral" ribs. A second type, also probably early in its development, is that seen in certain embolomeres, where a rather slender blade is developed anteriorly in addition to the rod-like posterior process. Here, I believe, a well-developed sacral rib articulated with the blade.[1] A further development from this type is that seen in seymouriamorphs, where the blade is expanded posteriorly so as to incorporate the rod-like region; with further evolution there results from this the iliac blade of reptiles, discussed by the writer on various occasions. Another type of iliac development is that seen in such primitive rhachitomes as *Eryops*, where the vertical blade is well developed and articulates with a single sacral rib, but the posterior process (probably as the result of reduction) is represented merely by a small spike. In other genera, presumably more advanced, even this last has disappeared.

The acetabulum, in labyrinthodonts as in primitive reptiles, is a large oval, centered in a triangular area formed by all three girdle elements. All well-preserved specimens exhibit a prominent buttress at the upper margin of the acetabulum. Below the acetabulum an elongate plate for muscular insertion is formed by the conjoined pubis and ischium. This faces ventro-laterally; the pubic portion tends to face more strongly ventrally than the ischiadic. The upper, inner surface of the pubis forms a triangular area, with its apex near the acetabulum, from which an important limb muscle (pubo-ischio-femoralis internus) took origin; a ridge usually marks off sharply this area from the remainder of the inner aspect of the girdle. A nerve opening (obturator foramen) pierces the girdle in the pubic region, its internal opening lying high up in this triangular area. The thickness of the pubis beneath this triangular region is highly variable. In *Seymouria* and the embolomere *Archeria*, for example, the pubis is a relatively thin (but broad) sheet of bone, with the outer surface facing well ventrally; in *Eryops* the outer surface faces much more laterally, and the bone beneath it is consequently much thickened. Variations possibly of utility in diagnosis are seen in the

[1]Although Watson (1926, p. 236) would disagree with this; further evidence is needed.

symphysis, particularly in the thickness of the opposed surfaces in various regions, but the facts are known in but few cases.

The humerus (cf. Watson 1917; Romer 1922; Miner 1925) is built on an essentially tetrahedral pattern common to both labyrinthodonts and early reptiles. In large forms with sturdy limbs, the great development of articular and muscular processes produces (as in *Eryops*) a bone without a shaft region; in smaller forms, or those with feebler limbs, some shaft development is evident. Proximal and distal planes of the bony surfaces may be, as in *Eryops*, "twisted" into a position nearly at right angles to one another; in other forms, the two ends may be nearly in the same plane. The proximal articulation, when well ossified, exhibits an elongate spiral surface suited to articulate with the characteristic glenoid fossa. There is always a prominent deltopectoral crest, and frequently a projecting supinator process is present distally on the radial margin. This latter process may, however, be reduced or fused into a longitudinal ridge along the distal part of this margin of the bone. Beneath the ectepicondyle lies a rounded convex articular surface for the radius; medial (or posterior) to it a rounded terminal area articulates with the sigmoid notch in the ulna. The entepicondyle is always well developed. In primitive reptiles this encloses a characteristic entepicondylar foramen for a nerve and vessels. This was long unreported in typical labyrinthodonts and hence was considered to be an advanced reptilian feature. It is however now reported in the rhachitome *Dendrerpeton* and the embolomere *Archeria* as well as in *Seymouria*, and it may be suspected that its presence was a characteristic feature of primitive tetrapods.

The labyrinthodont femur (cf. Romer 1922) is characteristically a cylindrical structure, somewhat expanded proximally and distally and with ridges or tuberosities developed ventrally. The head bears a crescentic articular surface dorsally; a prominent fossa is present proximally on the ventral surface. Anterior to the fossa is a trochanter analogous to the pectoral crest of the humerus. A Y-shaped system of ridges usually leads down the shaft from the trochanter and from the opposite margin of the fossa. At the union of the two branches there is typically a fourth trochanter for the attachment of caudifemoral musculature; the distal "stem" of the Y is presumably for the attachment of adductor musculature. There is considerable variation, of diagnostic value, in the development of the various parts of the ridge system and of the associated trochanters. Distally the femur is more or less bifurcated, with two condylar areas ventrally for the

head of the tibia and, at the lateral edge of the outer condyle, a crescentic area for the attachment of the fibula.

Radius and ulna, tibia and fibula are sturdy if short elements with prominent morphological features. They have, however, been accurately described in so small a series of forms as to make them valueless at the moment for our purposes.

The structure of manus and pes should be extremely significant in evolutionary studies. But, as might be expected, this is known in very few cases and, even when found in articulated condition, much or all of the carpus and tarsus is often seen to have remained unossified. One of the few well preserved and well described specimens of the carpus is that of *Eryops* (Gregory, Miner and Noble 1923). The carpal arrangement seen here is generally believed to be a primitive one. Twelve elements are present. Three proximal ones include radiale, intermedium and ulnare; there are four centralia, three of them ranged inward from the radial margin, the fourth occupying a central position in the carpus; distally one element articulates with each proximal phalanx.

Data on the tarsus have been recently summarized by Schaeffer (1941). The arrangement is apparently basically similar to that of the carpus. Even in *Seymouria*, apparently, the amphibian type differs from that in even the most primitive of reptiles in the presence of three elements in the proximal row. .

The number of digits and of phalanges per digit in manus and pes is a feature which might be both important and diagnostically useful in labyrinthodont evolution and classification, were it not that the formula is known in only a handful of examples. Living amphibians have but four digits in the manus, and the same condition holds, as far as now known, in the temnospondyls. In the Anthracosauria, the only well known cases — *Diplovertebron* and *Seymouria* — exhibit a five-fingered manus, as do the reptiles. It has been frequently assumed that the lower number is the primitive one, but the converse may well be the actual situation; and both embryological data and the build of the *Eryops* carpus suggest that an even higher number may have been present in the development of a fixed digital pattern from a fin of crossopterygian type. In the pes, five digits are, as far as known, always present.

Phalangeal formulae are seldom certain. In general the formulae are below that of reptiles — *Seymouria* is a conspicuous exception — and such formulae as 2.2.3.2 for the manus and 2.2.3.4.3 for the pes seem to be common among the temnospondyls.

DERMAL ARMOR

Too little is known of dermal armor in most cases to make this series of structures of any great use in phylogenetic discussion. In all, or nearly all, labyrinthodonts in which armor is known, there is a characteristic ventral covering, between pectoral and pelvic girdles, of V-shaped rows of overlapping quadrilateral scales. Since the structure is essentially similar in forms as far apart as embolomeres, ichthyostegals, eryopsids and brachyopids, this retention of a fish-like ventral squamation is presumably a primitive and rather general feature. However, there is no evidence of this type of ventral armor in typical seymouriamorphans; and it is not impossible that reduction may have taken place in other groups as well.

There seems to have been, in general, a strong trend for reduction of the original armor on the back and sides of amphibians, and in relatively few cases do we have any evidence of conditions in this area. There are, however, a number of instances — such as *Archegosaurus* and *Scleroccphalus* (Broili 1927a) and *Eryops* (Romer and Witter 1941), where rounded or oval dorsal scales, reduced in degree of ossification, are known, and it may be that such scales, buried in a tough hide, were present among labyrinthodonts generally.

In a few cases — as the semouriamorph *Kotlassia* and the dissorophids—there is a redevelopment of dermal ossification in the form of a dorsal armor, similar in a general way to that which tended to develop in various higher tetrapod groups.

SCLERAL RING

In various labyrinthodonts in which preservation has been favorable, a bony scleral ring of 20 to 32 plates has been described in the orbit (Edinger 1929). This is in agreement with a comparable high count in crossopterygians; in reptiles and in lepospondylous amphibians the number of plates is smaller, and these structures are absent in modern amphibians.

ICHTHYOSTEGALS

The Ichthyostegalia was founded (as an order) by Säve-Söderbergh, to include only the two ichthyostegid genera of the late Devonian(?) discussed just below. To it, however, there appear to belong certain Carboniferous types — *Otocratia*, *Colosteus* and *Erpetosaurus*. It is further quite possible that the earlier Devonian form *Elpistostege* is an ancestral ichthyostegid.

Ichthyostega, Ichthyostegopsis

(Figs. 15, 16)

These genera are from beds in East Greenland which, as noted in the stratigraphic section, lie close to the Devonian-Carboniferous boundary; they are thus the oldest forms which are to be included with certainty among the Amphibia. They were first reported by Säve-Söderbergh in 1932; an account was given of the dermal elements of the skull roof and some data on the palate. Unfortunately he has been unable to publish a more comprehensive description, and we are thus in nearly complete ignorance of the structure of the lower jaw, braincase and postcranial skeleton.

The skull roof was described in detail, using a nomenclature discussed in an earlier section. It is obvious from the author's illustrations

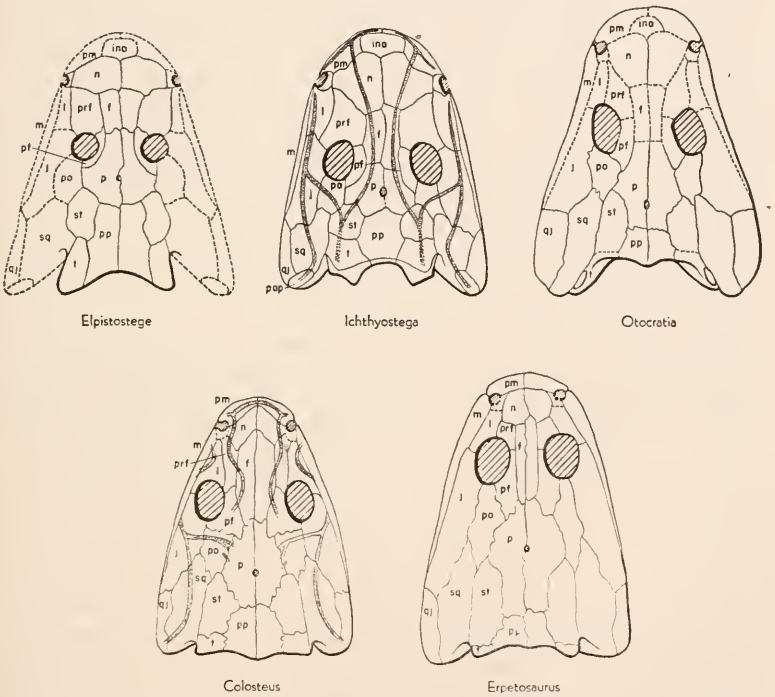

Fig. 15. Skull roofs of ichthyostegals. *Elpistostege* restored after Westoll; *Ichthyostega* after Säve-Söderbergh, Westoll; *Otocratia* after Watson.

that his restorations and interpretations might be subject to revision in certain points; Westoll (1943) has published a revised restoration, using the customary amphibian bone nomenclature.

In contrast to most later amphibians, but in agreement with conditions in ancestral fishes and in early reptiles, the skull is relatively high and with rounded contours — indeed, so well rounded that, for example, the narial region is invisible in dorsal view unless arbitrarily flattened (as in our figure). The facial segment of the skull is relatively short, the skull table much more elongate than in most later labyrinthodonts — proportions suggestive of a transition from the crossopterygians, with their inordinately long post-orbital skull region. The otic notch is modestly developed, and a significant feature is that the cheek is firmly attached to the table, as in the general temnospondyl group and in contrast to the embolomeres. A feature emphasized by Säve-Söderbergh is the nature of the external naris. This is extremely lateral in position, and open along the rim of the jaw — premaxilla and maxilla fail to meet. This condition is reasonably interpreted as a primitive one. There is no indication of the transverse "break" in the roof which is seen in typical crossopterygians and is there associated with the underlying joint in the braincase. In contrast with many other early amphibians, but in agreement with genera discussed later in this section, the quadrate region is not far behind the plane of the occiput.

In ichthyostegids, almost uniquely among amphibians, the lateral line organs still lie in closed bony canals as in bony fishes, rather than in grooves in typical amphibian fashion.

The general pattern of the roof is comparable to that of later labyrinthodonts, but there are various features of a primitive or possibly aberrant nature. An internasal element survives on the rostrum as a representative of the complex of elements found on the snout in crossopterygians. A superficial element lying medial (or dorsal) to the external naris — Westoll's postnarial — appears to represent the septomaxilla in a primitive stage of its history. The prefrontal is very large; Westoll confirms my interpretation (Romer 1933, fig. 95) of this structure as being a single element, rather than two as restored by Säve-Söderbergh. The lacrimal does not enter the narial margin, from which it is separated by the septomaxilla. The persistence of a small preopercular bone at the posterior margin of the cheek is a surprisingly primitive, piscine, feature. In the skull table, the much elongated postparietals appear to have formed a single median element and in one instance, at least, the parietals are

likewise incompletely separated. As in temnospondyls generally the tabular has no contact with the parietal. There is a well developed supratemporal but no intertemporal; much of the area which the latter covers in many early labyrinthodonts is here occupied by a broad lateral extension of the parietal. It will be noted that there is, in consequence, no contact between the postfrontal and the temporal elements, a feature contrasting sharply with the usual labyrinthodont arrangement.

The palate is incompletely described, but appears to have been in most regards of the primitive type seen in embolomeres, seymouriamorphs and loxommids, with interpterygoid vacuities practically absent, a broad palatal expansion of the pterygoid and a freely movable basal articulation with the braincase. There is an anterior palatal vacuity. The narial region is, as noted, unusual in construction in the lack of maxillary-premaxillary contact; this is compensated by a union of maxilla and vomer to form a bar which separates external and internal bony narial orifices.

Little is known of the lower jaw, and the data seen in Säve-Söderbergh's figures are inadequate for a discussion of the braincase. The occipital condyle appears to have been single. The teeth are labyrinthine in structure. The lack of contact between maxilla and premaxilla breaks the continuity of the marginal tooth row. The longest teeth appear to have been those in the posterior part of the premaxilla; there is a suggestion of another peak in tooth size in the maxilla. The palatal dentition is incompletely known.

There is no indication in the description as to whether any postcranial material was found. There is thus, at the moment, no actual evidence that the ichthyostegids are truly tetrapods rather than some advanced fish type. However, as will be seen below, seemingly related Carboniferous genera exhibit a typically amphibian postcranial structure.

Otocratia

(Fig. 15)

In his original description of the ichthyostegids, Säve-Söderbergh gave no indication of their possible close relationship to other known amphibians. It is apparent, however, that there are several Carboniferous forms which belong to the same general group. One such is *Otocratia*. This genus is represented only by a single incomplete

skull from the Burdiehouse Limestone of Scotland. This limestone is at a relatively low level in the Lower Carboniferous system of that country and *Otocratia* is older than any non-ichthyostegal labyrinthodont.

As described by Watson (1929, pp. 227–229, figs. 5, 6) it exhibits the contours of the skull roof, but shows the sutures only in the post-orbital region. It has long been apparent to the writer that this form is closely comparable to the ichthyostegids, and Westoll (1942) has independently arrived at the same conclusion. As in the ichthyostegids, the temporal region is elongated, the face relatively short and the eyes are well forward. The postparietals are greatly developed; they are paired, as in amphibians generally and in contrast to conditions in known ichthyostegid specimens. The tabular

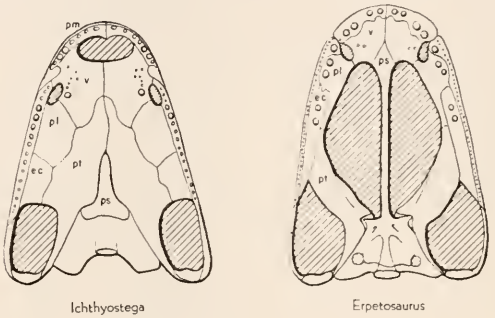

Fig. 16. Palates of ichthyostegals. *Ichthyostega* after Säve-Söderbergh, Westoll; *Erpetosaurus* after Romer, Steen.

does not touch the parietal. There is no intertemporal; the supratemporal is highly developed but is separated from the postfrontal by a lateral expansion of the parietal, as in the ichthyostegids. The material is inadequate to show whether or not a preopercular was present. We know little about the anterior portion of the skull roof except the position of the external naris. This appears to have been closed laterally by union of premaxilla and maxilla, but it is significant that the naris is in an extremely lateral position (cf. *Erpetosaurus* and *Colosteus*, below), as if the union of these bones had occurred at a stage but slightly earlier. As Westoll suggests, and as I had also concluded, the opening which Watson thought to be an internal naris is probably an anterior palatal vacuity which (as in the case of a similar opening in the ichthyostegids) lodged the tip of an an-

terior mandibular tusk. Of the dentition, only a few premaxillary teeth are preserved. Their nature is probably significant. The anterior ones are small; posteriorly there is an enormous premaxillary tusk (cf. the large premaxillary teeth in *Ichthyostega*).

A peculiar feature is the development of the otic notch region. The tabular extends laterally and ventrally to fuse broadly with the squamosal (? and pterygoid) so that the former notch becomes a tubular opening of small diameter. Otic notch closure is witnessed in several later labyrinthodont groups, but the fashion of closure is quite different from that seen here. It is reasonable to believe that in early amphibians, considerable "experimentation" occurred in the structure of newly developing mechanisms of sound reception. With the unusual otic structure of *Otocratia* in mind, it will be seen that the ichthyostegid materials suggest the initiation, if not the completion of a similar structure (*Ichthyostega watsoni*, "ichthyostegid sp. a", Säve-Söderbergh 1932, pls. 5, 6, etc.).

In almost every feature it has been seen that *Otocratia* is closely comparable to the ichthyostegids. There has, however, been some shortening of the extreme posterior portion of the skull table and particularly of the tabular bone; one might suspect some advance in palatal construction, but evidence is not available.

No other labyrinthodont genera have been described from the Burdiehouse and hence it is quite possible (but by no means certain) that two other specimens from this locality which appear to be labyrinthodont in nature belong to this genus. Lydekker (1890, pp. 158–159) notes (but does not figure) a palate from Burdiehouse which he assigns — most improbably — to a much later labyrinthodont, *Anthracosaurus russelli*. I am not familiar with the specimen and Lydekker says little concerning it except to note the presence of palatine and (?) ectopterygoid tusks. If the specimen is actually similar to that of *Anthracosaurus*, the palate is of the primitive closed type common to ichthyostegids, loxommids and anthracosaurs generally. Lydekker (1890, p. 165) further notes an interclavicle from this locality which he refers to *Loxomma* because of its similarity to one provisionally referred to that genus by Huxley. He gives, however, little data on the specimen except to indicate his belief that a stem had been present.

Watson believed *Otocratia* to have been an embolomere, but no vertebrae are associated, and the suggestion was made only because of the then reasonable belief that Carboniferous labyrinthodonts generally possessed such vertebrae.

Erpetosaurus, Colosteus

(Figs. 13, 15, 16)

These genera are among the commonest forms in the fauna from the Upper Pennsylvanian (Westphalian C) cannel coal of Linton, Ohio. The material, originally described by Cope, has been redescribed by Romer (1930, pp. 100–114) and Steen (1931, pp. 852–860). Upon the publication of the descriptions of the East Greenland ichthyostegids, it was at once apparent that we were here dealing with late members of the same group.[1] Discussion of them may be undertaken in the light of this relationship. The two genera are unquestionably distinct and differ in skull proportions and certain other features, but they appear to be fundamentally similar in structure and may be treated in common. In both genera we find skull proportions of the sort seen in the ichthyostegals already considered — the face short, the skull table much elongated, and the orbits, in consequence, well in advance of the middle of the skull length. In *Otocratia* the orbits were moderately in advance of the mid-length; in *Colosteus* the table is somewhat more elongate; and in *Erpetosaurus* the table is very elongate, the face extremely short. Proportions similar to those of the last genus are found in certain later rhachitomes and stereospondyls (as *Trimerorhachis* and the metoposaurs), but the dermal bone pattern is a different one, and there is surely no genetic connection.

The otic notch is, as in ichthyostegids, shallow. The cheek appears to have been fairly firmly connected with the skull table, and in *Colosteus*, apparently, but not in *Erpetosaurus*, the squamosal has a contact with the tabular as in older genera. The narial region is poorly known in detail but, as may be seen from figures of the various specimens, the external naris was (as in ichthyostegids) extremely marginal in position; there was at the most a weak union of premaxilla and maxilla lateral to it. It is probable that the septomaxilla persisted in maintaining a superficial position medial and posterior to the naris.

Most significant in connection with the ichthyostegid affinities of these genera is the pattern of the temporal region. As in ichthyostegids, the intertemporal is absent and the supratemporal, although

[1]They were classified together in the writer's "Vertebrate Paleontology" (1933, p. 437). Since, however, *Erpetosaurus* and *Colosteus* were then considered as branchiosaurs, the ichthyostegids were quite naturally given the dubious honor of admission to that nonexistant order, the Phyllospondyli.

well developed, is widely separated from the postfrontal. The tabulars are (as in *Otocratia*) considerably reduced in area from the conditions seen in *Ichthyostega*, but the postparietals are still very prominent — particularly so in *Colosteus*. In both genera the postparietal is paired, as in *Otocratia* but in contrast to the ichthyostegids. It may be noted, however, that Steen failed to find a median suture in the parietal region in two specimens of *Erpetosaurus*, suggesting a retention of the tendency toward fusion of median elements noted in ichthyostegids.

The postorbital is peculiarly developed. In these genera, as in other ichthyostegals, this bone extends far back from the orbit, with its center of ossification well back of the orbital rim. In *Erpetosaurus* (as in *Otocratia*) the bone constricts in width anteriorly and participates only to a minor extent in the orbital boundary; in *Colosteus* it has withdrawn completely from the rim of the orbit, and has become an element of the temporal region, with a deceptive similarity to an intertemporal.

The lateral line system is well developed in *Colosteus*; it occupies a system of grooves in typical amphibian fashion, and in contrast with the piscine canal system of *Ichthyostega*.

The palate is incompletely known in *Colosteus* but rather adequately preserved in *Erpetosaurus*. The persistence of a movable basal articulation is a primitive feature; but in marked contrast with the ichthyostegids, there are very large palatal vacuities, larger than those of the average rhachitome; palatal evolution has here paralleled that of the rhachitomes, and moved at a faster pace. The pterygoids did not reach far forward on the palate. The disposition of vomers, palatines and ectopterygoids is of normal nature. The first appears to have carried a tiny pair of teeth, the ectopterygoid a typical pair of large tusks. Both Steen and the writer have restored a row of three large teeth rather than the usual pair in the palatine region. Steen believes that all three were on the palatine; the writer's material suggested to him that the most anterior was an anomalous structure — a maxillary fang internal to the tooth row, which may have arisen from the ichthyostegid condition in which the maxillary row turned inward posterior to the naris.

The anterior end of the palate is imperfectly known. In *Colosteus* there appear to have been a few small anterior premaxillary teeth, followed by a pair of very large ones, comparable in size to typical palatal fangs; so great is their size that the outer surface of the lower jaw is seen in several specimens to be grooved for their reception.

In *Erpetosaurus* my material showed nothing but the presence of a similar large tooth or tooth pair in the anterior part of the upper jaw; as in *Colosteus*, the lower jaw is grooved for its reception. Steen had a single specimen representing this region which she interprets as showing on each premaxilla two pairs of large fangs, no smaller teeth being present. The presence of large premaxillary tusks is suggestive of the situation in *Otocratia*.

Certain structural features are seen in the ventral view of the braincase, including: the entrances to carotid canals; fenestrae ovales; a single occipital condyle; a moderate ventral expansion of the body of the parasphenoid; an elongate and moderately flattened cultriform process of the last element which ends anteriorly, as in many temnospondyls, in a V-shaped expansion between the vomers.

The lower jaw appears to show certain unusual features, but the structure is as yet inadequately known.

Little postcranial material has been found with most of the skull specimens. Small skeletons termed *Odonterpeton triangularis* and *Tuditanus minimus* may be young individuals of *Erpetosaurus*, but little can be determined from them. Specimens of *Colosteus*, such as one figured by Cope (1875, pl. 36, fig. 1), show the presence of a well developed abdominal armor and of tetrapod limbs of modest size, and *Erpetosaurus* appears to have had a similar ventral squamation as well as rounded dorsal scales. Various specimens show the presence of clavicles and interclavicles which were broadly developed and sculptured ventrally; the interclavicle was rather elongate but not stemmed. Steen has described various isolated limb and girdle elements, notably an ilium with a rod-like posterior process but lacking any expansion of the blade. Vertebral structure has been a matter of doubt. The writer suggested that vertebrae of the *Molgophis* type belonged here, but Steen pointed out (quite properly) that this was improbable. She described as presumed vertebral elements isolated triangular plates suggestive of a rhachitomous condition.

A skeleton of *Erpetosaurus* which I hope to describe in detail on some future occasion contributes greatly to our knowledge of the postcranial skeleton — knowledge highly desirable because of our complete lack of information on the skeleton of other ichthyostegals. The girdles and limbs are nearly completely preserved. Of especial interest is the presacral vertebral column, exhibiting a connected series of neural arches with low rounded summits. The structure of the centra requires further study. However, it is definitely neither embolomerous nor phyllospondylous and consists of triangular and

polygonal elements — in great measure displaced — indicative of a rhachitomous condition.

From the description above, it seems reasonable to believe that we have in *Colosteus* and *Erpetosaurus* late-surviving members of a phyletic line of which the ichthyostegids were earlier representatives; the palatal construction, however, indicates that considerable evolution had taken place within the group. The postcranial material is of importance, since nothing apart from the skull is known in other forms.

Elpistostege

(Fig. 15)

This genus is known only from a single specimen, a partial skull roof from the famous Scaumenac Bay Devonian fish locality in eastern Canada (Westoll 1938; Romer 1941; Westoll 1943). The specimen includes most of the central portion of the roof. Westoll has restored the marginal regions rather along crossopterygian lines; however they can be readily restored in amphibian, and specifically ichthyostegal fashion, as I have done here. Westoll has rightly commented on the importance of the specimen as demonstrating the transition from crossopterygian skull proportions — with an extremely short "face" and greatly elongated skull table — to those of tetrapods; the writer (1941) has further developed this point. The elongate condition of the skull table seen here is quite surely that to be expected in any primitive tetrapod; it is, however, particularly suggestive of the present group, in which the tendency for the retention of this condition is especially marked. This does not in itself give reason for the inclusion of *Elpistostege* in the Ichthyostegalia. But it will be noted that in the temporal region we see the most diagnostic feature of the ichthyostegid skull — absence of the intertemporal, and the wide separation of postfrontal and supratemporal by a lateral extension of the parietal. *Elpistostege* may thus be reasonably considered as at least ancestral to the ichthyostegals, and very probably belonged to this group, although (as would be expected from its early appearance and presumably transitional nature) the elongation of the table, and particularly of the (paired) postparietal and tabular elements, is greater than in any of the later genera. The nature of the otic notch cannot, of course, be precisely determined; but the fact that the cheek region has been disarticulated indicates a relatively loose attachment of cheek to

table, in contrast to the closer union seen in rhachitomes generally as well as in later ichthyostegals. Since the attachment appears to have been a loose one in osteolepid crossopterygians, this feature is presumably a primitive one, which does not debar *Elpistostege* from ancestry to and close affiliation with the ichthyostegals.

It is to be hoped that further data may be obtained regarding this interesting genus, since it might shed much light on the transitional stages, in posteranial skeleton as well as skull, between rhipidistians and the developing amphibian groups.

DISCUSSION

The genera reviewed above show, as we have seen, certain structural features which are not found in any other amphibians and which therefore strongly suggest that they may be considered as members of a common group, for which Säve-Söderbergh's term Ichthyostegalia is available. Because of the limited material known, the diagnosis must be confined to features of the skull roof, and particularly the table. An elongate table was presumably characteristic of the earliest amphibians of all sorts. However, the retention (in contrast to secondary re-development) of the elongate condition is not seen in labyrinthodonts of any other groups, and when a secondary lengthening takes place, the postparietals are not markedly elongated. Most significant of ichthyostegal features is the condition of the temporal region, repeatedly emphasized above — the absence of the intertemporal, and the lack of contact of supratemporal with postfrontal. This condition is found elsewhere only in two relatively late and obviously non-primitive forms (*Dvinosaurus, Broomulus*). The extreme lateral position of the external naris is presumably a diagnostic feature, as is the retention of the primitive single skull condyle and a movable basipterygoid articulation. The dentition appears to show features which are possibly diagnostic but more data is needed.

Within the Ichthyostegalia, however, there certainly occurred marked evolutionary changes, as might be inferred from the long span of time covered by their known history, and as can be definitely proved in certain points. A notable change is that seen in the palatal construction, which in the ichthyostegids was of the primitive closed type, but in colosteids exhibits palatal vacuities as large as those of advanced temnospondyls. Although the table is elongate in all cases, there is a tendency for some reduction in length, and, beyond the Ichthyostegidae, a relatively great reduction in the development

of the tabulars. Modifications of this sort suggest that several subordinate groups may be present within the Ichthyostegalia. The very great elongation of the table and the seemingly loose articulation of the cheeks are known features in which *Elpistostege* differs from later genera. Palatal development is a significant feature in which the colosteids differ markedly from the Ichthyostegidae. The position of *Otocratia* is not entirely clear, in default of data on the palate, but the reduction in size of the tabulars suggests closer affinities with the colosteids.

That the Ichthyostegalia are apsidospondyls and members of the Labyrinthodontia, in the broad and current use of that term, seems clear from the nature of the vertebral column seen in *Erpetosaurus*. The essentially rhachitomous type of vertebral construction seen here was present also in known rhipidistians and there is hence no reason to believe that earlier ichthyostegals had a vertebral structure markedly different in nature.

As noted in the introduction, current knowledge of labyrinthodont structure and evolution suggests that the group may be divided into two superorders: the Anthracosauria, including embolomeres and seymouriamorphans, and the Temnospondyli, using that term to include the characteristic rhachitomes and the derived stereospondyls. The Ichthyostegalia on the basis of vertebral structure may reasonably be included in the second of these groups. Additional key characters of the temnospondylous division are to be found in the "loxommoid" pattern of the skull roof, emphasized by Säve-Söderbergh and Steen, in which the tabular is small and lacks contact with the parietal, and the cheek is firmly fused with the skull table. These characters also are found in the present group (except for the presumed loose cheek of *Elpistostege*).

Although the Ichthyostegalia may be viewed from one aspect as a self-contained group of labyrinthodonts, the relatively great antiquity of the group must be kept in mind; as was noted, all the ichthyostegal genera, except the colosteids, are older than any other known labyrinthodonts of any sort, and if *Elpistostege* be included here, the order can be traced back to a time at which the development of amphibians can have barely been initiated. We must thus consider the earlier ichthyostegals in the light of their possible relationship to other tetrapod groups.

Certain features of the order, such as table elongation, and, in *Elpistostege*, the presence of a movable cheek articulation, are primitive features to be expected in the ancestry of any amphibian group.

They indicate that the Ichthyostegalia are primitive forms, presumably, in their earlier genera, not far removed from the ancestral amphibian type. If, however, we attempt to place the Ichthyostegalia on the line of ascent to any later labyrinthodonts, difficulties at once appear.

It is difficult to consider them as ancestors of later groups of the Temnospondyli, even though we here consider them as the oldest subdivision of that group (cf. Säve-Söderberg 1932, p. 104 etc.; 1935, pp. 11–12). In most temnospondyls the intertemporal is lacking, as it is in ichthyostegals. But both in loxommids and "normal" rhachitomes, certain of the older and seemingly more primitive types possess an intertemporal, which later is reduced or absent. This element is apparently not a neomorph, but was very probably present in the rhipidistian ancestors as the dermosphenotic. Further, even if the intertemporal is lost, the postfrontal-supratemporal contact persists in almost every temnospondyl. In these features the ichthyostegals are obviously aberrant, and must be considered as a side-branch (although a very early one) of the rhachitomous stem.

It is still more difficult, of course, to consider the Ichthyostegalia as in any way ancestral to the Anthracosauria. It is possible that the vertebral type of the embolomeres and seymouriamorphans was derived from an early rhachitomous stage; but the lack of the intertemporal, ubiquitous in anthracosaurs, the small size of the tabular and (except in *Elpistostege*) the firm fusion of cheek and table are all features in which the ichthyostegids are markedly different from and seemingly more specialized than the anthracosaurians.

It seems not improbable, as Westoll (1942) has noted, that the early ichthyostegals might have been related to the ancestry of certain, at least, of the lepospondyls — using that term in a broad sense — and particularly to the varied series of lepospondyls often termed microsaurs (including Watson's Adelospondyli). Never is there in this group an intertemporal; in fact, there is, in the microsaurs at least, further reduction, so that the entire area of the "temporal" and tabular region is occupied by a single bone, perhaps best termed supratemporal. Such a condition might have been derived from that seen in the Ichthyostegalia by a continuation of reduction of elements in the temporal region. A comparison of the colosteids or *Otocratia* with such an early microsaur as *Dolichoparcias* (Watson 1929, pp. 247–249, figs. 26, 27) is of interest. The three elements termed by Watson postorbital, supratemporal and squamosal appear to the writer to be, respectively, postfrontal, postorbital and supra-

temporal. The skull proportions of *Dolichoparcias* and *Erpetosaurus* are exceedingly similar although they may, of course, merely mean the retention or exaggeration of a primitive pattern in two very diverse lines. In *Dolichoparcias*, exactly as in *Colosteus*, the postorbital has been excluded from the orbital margin. The vertebral construction is markedly different, but presumably the lepospondylous construction has arisen as a secondary condition from a rhachitomous (or proto-rhachitomous) column. On the whole, it is not at all impossible that the early ichthyostegals were a group from which the microsaurs originated.

Westoll (1942, 1942a) has suggested the origin of certain, at least, of the reptiles from an ichthyostegal form (*Otocratia*) *via* microsaurian lepospondyls. I am not convinced that there is any relationship between microsaurs and reptiles, and believe the resemblances due to convergence; we may, however, consider the possibility of a more direct connection between the ichthyostegals and ancestral reptiles. As I am pointing out elsewhere, the cotylosaur *Limnoscelis* is a form which appears to lie close to the base of the reptilian stock. The vertebral structure of *Limnoscelis* and, indeed, its entire postcranial anatomy, shows strong similarities to that of the Seymouriamorpha and indicates close relationship to that group. This would imply descent of reptiles from forms with an anthracosaurian type of skull roof. But in *Limnoscelis* the intertemporal, characteristic of every known anthracosaur — embolomere or seymouriamorph — is absent; the parietal is expanded laterally and has a broad contact with the postorbital, while the supratemporal is widely separated from the postfrontal. This is the situation which we have seen present in ichthyostegals. It suggests the possibility of the descent of reptiles from the early ichthyostegals. But no other features of that group, as far as known, suggest an intimate relationship. It is possible that the numerous resemblances in other features — particularly vertebral structure — between seymouriamorphs and cotylosaurs are attributable to either retention of primitive tetrapod structures or to parallelism. It is possible, but at present seems highly improbable; and until our knowledge of postcranial evolution in amphibians is far more advanced than at present it seems more reasonable to consider that the similar build of the temporal region in ichthyostegals and reptiles has been acquired independently.

Known ichthyostegals are few in number, and in consequence we might tend to consider the group one of little importance in the life of the Paleozoic. We may note, however, that their life span —

from early Upper Devonian to Upper Pennsylvanian — covers more than two full periods, a longer time span than that of any other minor labyrinthodont group. Further, labyrinthodont remains of any sort are quite rare until a time close to that of the disappearance of the ichthyostegals. It is not improbable that the Ichthyostegalia were the first of various labyrinthodont stocks to obtain a dominant position, and that future discoveries will show that they flourished in a profusion of forms in the early Carboniferous.

LOXOMMIDS

The Carboniferous loxommids are a close-knit group, immediately recognizable because of their peculiar, keyhole-shaped orbits. Included are but five genera — *Loxomma*, *Baphetes*, *Macrerpeton*, *Megalocephalus* [*Orthosaurus*] and *Spathiocephalus*. Most of the forms were adequately described by Watson (1926, 1929).

Loxomma

(Fig. 17)

A common and primitive genus is *Loxomma*, known from several Mississippian and Pennsylvanian localities: the Gilmerton Ironstone of the Scottish Mississippian (*L. allmanni*) (Huxley 1862), the early Pennsylvanian of Airdrie, Scotland, (*L. acutirhinus*), and the late Pennsylvanian of Nyrany, Bohemia (*L. bohemicus*). The genus has been erroneously reported from various Coal Measure localities in England. *Loxomma* (Watson 1929, pp. 236–238) in most regards exhibits skull features characteristic of the group as a whole. The interorbital region and skull table are relatively narrow, the cheek region and snout relatively broad. The orbit proper is a subcirular area of modest size, but the orbital opening includes an expansion, anteriorly and laterally, which invades the lacrimal region and is generally assumed to be for the reception of some type of glandular structure. An analogous fenestration of the lacrimal region is seen in the Lower Permian rhachitome *Trematops*; in that case, however, the opening is a posterior extension of the naris rather than an anterior extension of the orbit. Apart from this feature, the cranial roof of *Loxomma* and its relatives is built on a pattern characteristic of rhachitomes of the late Carboniferous and early Permian. The squamosal is tightly bound to the skull table, in contrast with the

loose connection seen in contemporary embolomeres. In *Loxomma*, but not in other genera of the group, an intertemporal is present, the skull table in this respect being in agreement with typical embolomeres and primitive rhachitomes and in contrast with the ichthyostegals. The intertemporal is very tiny in *L. allmanni*, the oldest species, and apparently on the point of disappearance. The tabular is small

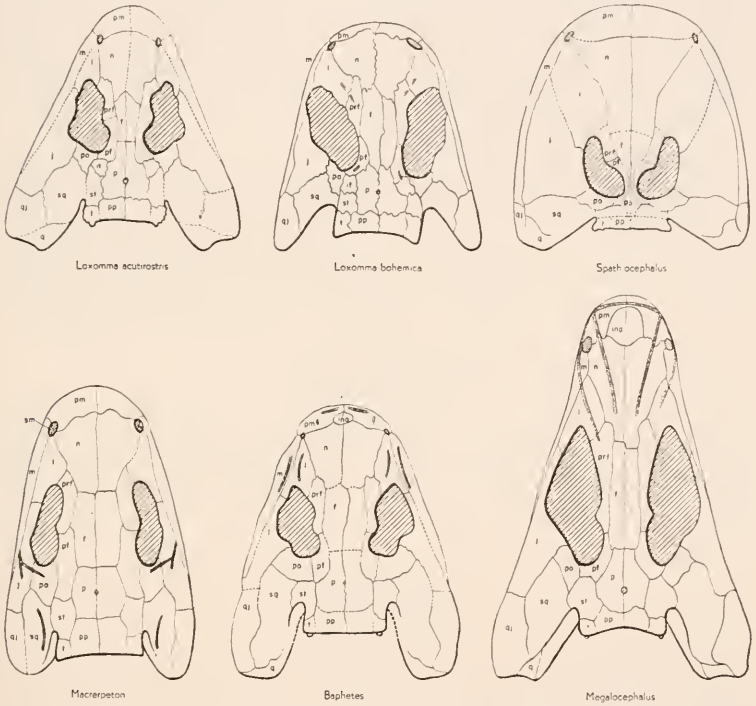

Fig. 17. Skull roofs of loxommids. *L. acutirostris*, *Spathiocephalus*, *Baphetes* after Watson; *L. bohemica* after Steen; *Megaloccphalus* after Atthey, Watson.

and excluded from contact with the parietals, as in rhachitomes and ichthyostegals and in contrast with embolomeres. The posterior margin of the tabulars bears a pair of small rounded bosses (cf. *Edops*). The large "cheeks" extend far back of the level of the occipital condyle. The anterior extension of the orbit occupies much of the region normally occupied by the lacrimal; this element reaches the region of the external naris. The naris is small and tends to be placed

close to the skull margin in loxommids, a position which, as noted in the discussion of the ichthyostegals, is probably a primitive one. No septomaxilla is reported in this genus, but in other loxommids this bone is present as a small superficial element at the posterior margin of the narial opening. In some loxommids a "rostral" internasal element, paired or unpaired, appears in the area of junction of the premaxillae and nasals; this is as yet unreported in *Loxomma*. In various members of the family traces of lateral line grooves are preserved, although in no instance are they extensively developed.

The palate is incompletely known in *Loxomma* but appears to have been similar to that of other genera.

No postcranial remains are known, and we may note that the same is true with regard to other loxommid genera. Huxley (1862, pl. 11) attributed to the Gilmerton specimen a pair of clavicles and an associated interclavicle from that locality. The specimen is of interest, the clavicles being well expanded ventrally and the interclavicle possessing a short truncated stem posteriorly. There is, however, no proof that this girdle belongs to *Loxomma* rather than to some other contemporary labyrinthodont.

Of the three species attributed by Watson to *Loxomma*, one, the genotype (*L. allmanni*), is Mississippian, *L. acutirhinus* is early Pennsylvanian, *L. bohemicus* (Steen 1938, pp. 237–239) very late Pennsylvanian. If the three are actually congeneric, the genus was a very long-lived one.

Baphetes

(Figs. 17, 19)

This somewhat more advanced genus is Pennsylvanian in age — mainly early Pennsylvanian (Watson 1929, pp. 238–241). *Baphetes kirkbyi* comes from Pirnie, Fifeshire; other species include *B. latirostris* from the early Pennsylvanian of Airdrie, Scotland, and *B. planiceps* from the late Westphalian coal deposits of the Pictou region of Nova Scotia. The first named species is represented by a complete skull, the second by a skull incomplete posteriorly, the third (Owen 1854a, 1855) by a snout only. The last form is, as Watson (1929, p. 238) notes, generically indeterminable — a situation particularly unfortunate since it is the genotype! *"Baphetes" minor* (Dawson 1870) is a jaw fragment from the Joggins, Nova Scotia, Coal measures, the systematic position of which is quite uncertain.

In most respects the skull roof of *Baphetes* is quite similar to that of *Loxomma*. A noteworthy distinction, however, is the fact that the intertemporal has disappeared; this genus and the remaining loxommids parallel the later members of the Rhachitomi in this regard. On the other hand, *Baphetes* shows an internasal rostral element.

The palate is well shown in this genus, particularly in *B. kirkbyi*. It is of a seemingly very primitive and generalized nature. As in typical embolomeres and the Devonian ichthyostegids the palate is of the "closed" type with little or no development of interpterygoid vacuities, and there are movable basipterygoid articulations. The vomers are large elements widely separating the small internal nostrils — an important diagnostic feature. Palatal fangs consist of single pairs of large tusks on all three lateral palatal elements. In this genus (and in *Loxomma*) there is no anterior palatal vacuity. The palatal construction is of a primitive type, comparable to that of ichthyostegals in various features, but in strong contrast with the embolomeres in the region of the nares and vomers.

Macrerpeton

(Figs. 17, 19)

This name has been applied by the writer (1930, pp. 119–126, figs. 19–22) to loxommid remains from the late Westphalian locality at Linton, Ohio. The type specimen of *Macrerpeton* [*Tuditanus*] *huxleyi* (Cope 1875, pl. 34, fig. 2) shows part of the skull roof and palate of a large loxommid. A smaller individual is represented by a nearly complete skull with jaws. The proportions of the elements present in the type are somewhat different; the two specimens may prove to be specifically or even generically distinct, but the differences may be related to growth and consequent changes in proportions. The skull, as restored from the smaller specimen, is very similar in almost every respect to that of *Loxomma* and *Baphetes*. It approaches the latter genus more closely and it is possible that the two genera are the same. The tip of the snout is not preserved, but if an internasal was present, it must have been of very small size. The intertemporal is absent; the postfrontal appears to have grown posteriorly to occupy its former position. The jaws are present in the smaller specimen, where they are seen from the external surface; they closely resemble those of *Megalocephalus*. The postcranial material which I once (1930, pp. 124–125) considered to belong to *Macrerpeton* probably pertains to *Colosteus*.

Megalocephalus

(Figs. 2, 10, 17, 19)

This appears to be the proper name for a large loxommid, the commonest of English Coal Measures amphibians, whose remains were in early years assigned to *Loxomma* and later described by Watson under the designation of *Orthosaurus*.[1] Excellent skull and jaw material is known from Newsham (Newcastle), and Watson (1929, pp. 240–241) lists other specimens from the Coal Measures of England (Fenton, Staffordshire; Coalbrookdale, Shropshire), the Palace Crag Ironstone of central coal field of Scotland and the earlier Pennsylvanian of Scotland (Airdrie, Pirnie). Watson (1929, p. 241) and Steen (1931, p. 886) note the presence at Linton, Ohio of one or more specimens similar to this form (but possibly assignable to *Macrerpeton*?).

In almost every structural feature of the skull *Megalocephalus* agrees with the genera described above. The skull is of very large size in the described specimens. It seems highly probable that in life the skull was large relative to the body size, for the braincase and tabular region of the skull are small, the cheek region greatly expanded and the facial region greatly elongated to give a relatively narrow snout. The intertemporal is absent. Lateral line grooves are well developed on the snout and a prominent paired internasal is present. The basic palatal structure is that seen in *Loxomma* and *Baphetes*; however, a large anterior vacuity, presumably for lower jaw fangs, is present. In other genera the braincase is poorly known. In *Megalocephalus* it is completely preserved but unfortunately little detail is available. The occipital condyle is a single structure. There are large posttemporal openings. A distinct supraoccipital bone is described, with the exoccipitals rising to the roof on either side of it. A small occipital flange, bearing a tubercle, is present on the tabular, but no occipital development of the postparietals appears to have taken place. The general construction of the occiput is not unlike that of the rhachitome *Edops*, in which, however, ossification was less complete.

The jaw has been described by Watson. In almost every respect it is of a type expected in a primitive tetrapod. The outer surface

[1] *Orthosaurus* Barkas is preoccupied, and Kuhn (1933, p. 37) proposed *Orthosauriscus* to replace it. However, Kuhn in his catalogue of the literature overlooks the alternative name of *Megalocephalus* Barkas 1873 (or, rather, gives it incorrectly as *Megacephalus*.) This generic name appears to be available; it is not considered a homonym of *Megalocephala* Tilesius. The first available specific name appears to be "*Pteroplax*" *brevicornis* Thomson and Young 1870.

shows a dentary and the four more ventral elements arranged in diagrammatic fashion. Internally the primitive three coronoids (apparently toothless) are present, and a well-developed prearticular. There is no retroarticular process. Several large fangs are present, but appear to be part of the marginal tooth row.

Despite the abundance of *Megalocephalus* remains, there is in no case any definite evidence of association of any postcranial material. At Newsham, where the genus is abundantly represented, various skeletal remains have been at one time or another attributed to "*Loxomma*", including for example a fine vertebral column. There is no proof of this association, and Watson now assigns most of the material to *Pteroplax* [*Eogyrinus*]. He is, however, inclined to associate vertebrae of embolomerous type with *Megalocephalus* because of the abundance of both *Megalocephalus* and such vertebrae at Newsham. But *Pteroplax*, also abundant there, was definitely embolomerous; if the *Megalocephalus* vertebrae were non-embolomerous, but (for example) rhachitomous, it is obvious that disarticulated central elements would be rarely observed and collected.

Spathiocephalus

(Fig. 17)

This name was given by Watson (1929, pp. 241–243) to a grotesque type of loxommid represented in the Lower Carboniferous of the Lonehead no. 2 ironstone in Scotland. The orbital pattern shows clearly its loxommid nature, but it is spectacular in the great breadth of the cheek region, which gives the skull a semicircular shape paralleled among later labyrinthodonts in several specialized end forms. It is of interest that this high specialization occurred at a relatively early stage of labyrinthodont evolution. The palate, except for its excessive breadth, appears to have followed the structural pattern seen in other loxommids. In contrast with the large marginal teeth common in Carboniferous labyrinthodonts the *Spathiocephalus* jaws bore numerous small chisel-like teeth comparable, as Watson notes, to those of "*Cricotus*" and suggesting similar piscivorous habits. Obviously, however, *Spathiocephalus* must have been an essentially bottom-dwelling form.

DISCUSSION

The loxommids are a compact group, varying tremendously in skull proportions but all exhibiting the one characteristic specializa-

tion of the orbits in combination with numerous cranial features which appear to be primitive. The skull pattern of (for example) *Loxomma* is, barring the orbital shape, in many ways that which would be expected in an ancestral tetrapod. It differs in two respects from the typical embolomere: (1) close union of cheek and table; (2) small tabular. In both respects the loxommids agree with ichthyostegals and typical Rhachitomi; the temporal pattern, however, clearly distinguishes them from the former, for an intertemporal was primitively present and a frontal contact is preserved by that element (or, in its absence, by the supratemporal); further, the post-orbital region is relatively short.

The palatal structure is of a diagrammatically simple pattern. The closed palate and movable basipterygoid processes are primitive features seen also in early ichthyostegals and in embolomeres and

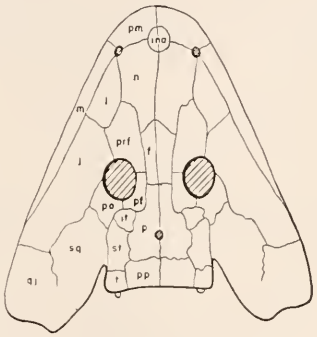

Fig. 18. The skull roof of *Loxomma*, modified by reduction of the orbit to normal proportions, for comparison with edopsoid rhachitomes.

presumably a direct fish heritage. The presence of broad vomers widely separating the nostrils is in agreement with ichthyostegids, rhachitomes and stereospondyls, and in contrast with typical embolomeres. The restriction of the larger palatal teeth to a pair on each of the three lateral palatal elements is exactly repeated in primitive rhachitomes and may well be primitive; in anthracosauroids the vomerine tusks are reduced. The jaw structure is presumably primitive. It must be emphasized that there is absolutely no positive evidence regarding the postcranial structure of any loxommid.

In sum, apart from the orbits, the loxommids are extremely primitive amphibians. An ancestor of the loxommids with normal orbits

(Fig. 18) could well have been an ancestor of the typical rhachitomes, and need only have developed its interpterygoid vacuities slightly to turn into such an animal as *Edops*. Watson placed the loxommids among the embolomeres, mainly because of their general primitive structure and the assumption that primitive Carboniferous labyrinthodonts were all presumably embolomerous. With our present knowledge of the diversity of Carboniferous vertebral structure, this assumption loses weight. It is highly probable that the loxommids are close to the ancestry of the rhachitomes and it is not at all

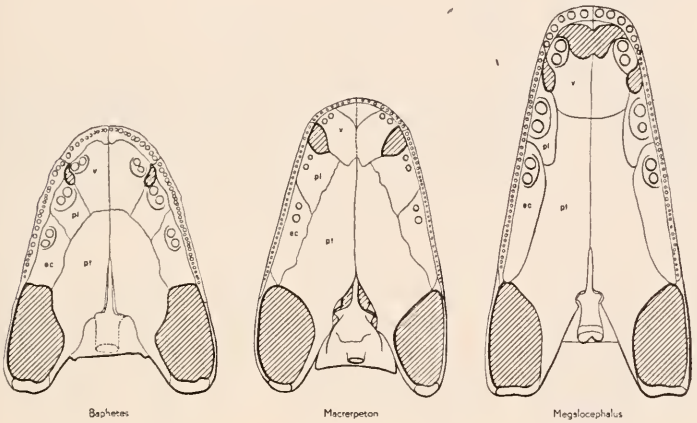

Fig. 19. The palate of loxommids. *Baphetes, Megalocephalus* after Watson.

unlikely that they may eventually be found to possess some type of rhachitomous vertebrae. How to classify them formally — particularly in default of knowledge of postcranial structure — is problematical. I suggest that they be provisionally included in a superfamily of Rhachitomi, the Loxommoidea, presumably ancestral to the other Rhachitomi and Stereospondyli and defined by the presence of primitively closed palates. Apart from the still hypothetical ancestors discussed above, the Loxommidae, as an early side branch, would be the only components.

It is difficult, in the absence of postcranial remains, to get any adequate conception of the life and habits of the loxommids. The skull proportions relating to skull table, braincase and occipital condyle strongly suggest that the skull was very large in proportion

to the body and that, hence these genera were mainly rather sluggish, persistent water dwellers. This conclusion is confirmed by the frequent presence of indications of lateral line grooves.

The finds of loxommids range from Upper Mississippian to Upper Pennsylvanian, with an apparent peak in the typical Westphalian Coal Measures. Apparently the loxommids replaced the ichthyostegals in mid-Carboniferous times as the commonest large inhabitants of the coal-swamp pools, only to become extinct — perhaps because of the competition of the typical rhachitomes — before the beginning of the Permian.

PRIMITIVE RHACHITOMES

Below are discussed various genera mainly of Carboniferous age, which appear to belong definitely to the rhachitomous group of temnospondyls, but are considerably more primitive in structure than the characteristic Permian members of this group. Truly primitive forms, here termed the Superfamily Edopsoidea, include: *Edops*, *Gaudrya* [*Nyrania*, *Capetus*], *Leptophractus*, *?Lusor*, *Dendrerpeton* and its allies (*Dendryazousa*, *Dendryskos*, *Platystegos*) and *Cochleosaurus*. Primitive but divergent and perhaps mainly larval or neotenous types are here considered as constituting the Superfamily Trimerorhachoidea; included are: *Eugyrinus*, *Pelion*, *Erpetocephalus*, various Carboniferous larvae, *Saurerpeton*, *Trimerorhachis*, *Dawsonia*, *Dvinosaurus* and *Chalcosaurus*.

Edops

(Figs. 2, 5–8, 20)

Best known of this group, as regards cranial structure, is *Edops craigi* (Romer and Witter 1942). This form is found in the lowest fossiliferous deposits of the Texas redbeds, in formations which now appear to be technically Permian in age; but close to the Pennsylvanian boundary. *Edops* appears to be a relict of a late Carboniferous fauna.

The animal was large, the best skull being the largest of any known Paleozoic amphibian. The skull pattern is typically rhachitomous in key features, such as the firm fusion of cheeks and table, small tabulars, and broad vomers, and indications of advanced conditions are seen in such features as the rather low contours of the skull and some development of cartilage in the supraoccipital and paroccipital regions. However, there are various structural points which are

suggestive of primitive conditions, appropriate to a labyrinthodont of Pennsylvanian rather than Permian age.

In the skull roof, a primitive character is the presence of a distinct intertemporal element, lost in characteristic rhachitomes. The tabulars bear rounded knobs reminiscent of those seen in the loxommids.

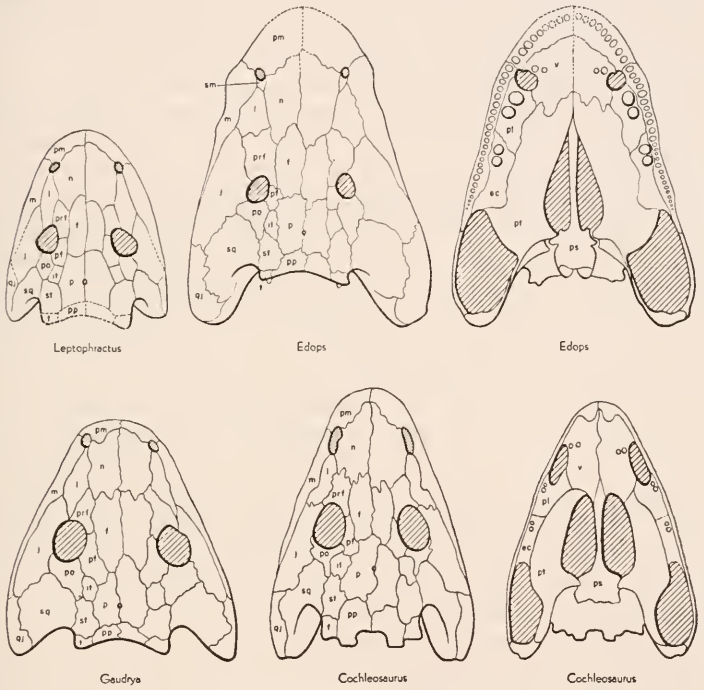

Fig. 20. Edopsoids. *Gaudrya* after Jaekel; *Cochleosaurus* after Steen.

The lacrimal is advanced in its withdrawal from the orbital margin, but a primitive feature of this region is the presence of a superficial, sculptured septomaxilla.

The palate is of the type already seen in ichthyostegals and loxommids, with the persistence of a movable basal articulation of epipterygoid and pterygoid with the braincase; interpterygoid vacuities are present, but they are of much smaller size than in typical rhachitomes, and a notably significant feature is that the two pterygoids are still broadly in contact in advance of the vacuities. The seemingly

primitive pattern of palatal tusks — a pair to each lateral palatal element — persists, although the anterior pairs, just in front of the broadly separated nares, are relatively small. The well preserved posterior part of the palate shows the epipterygoid to have expanded very widely above the pterygoid both anterior and posterior to the region of the basilar articulation, and to have been in broad contact posteriorly with a highly developed quadrate. This is a remarkably primitive condition of the endochondral palatal elements.

The anterior portion of the braincase is as a whole relatively much higher and narrower than in the "platybasic" type of braincase seen in *Eryops* and similar forms. As noted, there is, to some degree, a lack of ossification on the occipital aspect of the skull, but in general the braincase is highly ossified, with none of the gaps in the side walls or otic region seen in advanced temnospondyls. The ventral surface in the posterior region is rounded, showing little of the flattening (accompanied by expansion of the parasphenoid) which develops in later rhachitomes. There is no distinct supraoccipital ossification, but there was, instead, a cartilaginous plug. A primitive feature is the persistence of a single large occipital condyle, with much of the articular surface still carried by a well developed basioccipital.

The lower jaw has a rather flattened and broadened construction anteriorly, but is otherwise generalized. The postcranial skeleton is incompletely known. The vertebrae have a typical rhachitomous build. The humerus lacks an entepicondylar foramen. The proximal limb segments are powerfully developed; forearm and lower leg appear to have been relatively short. Numerous small nodular structures are presumably dorsal and lateral scales.

Edops, in the structural features recounted, might well be antecedent to typical Permian rhachitomes, but is far more primitive than any other rhachitome of that period. To find close relatives of *Edops* we must turn to Carboniferous forms.

Gaudrya

(Fig. 20)

A geologically older genus which appears to be closely related to *Edops* is a large amphibian from the late Carboniferous gas coal of Nýřany, Bohemia; its remains have been described under various names; *Gaudrya latistoma* appears to be the proper designation.

The best specimen of the skull roof is that figured by Jaekel on various occasions (1911, fig. 124; 1913, fig. 5). Jaekel compares this skull with *Chelydosaurus vranii*, to which, however, it is not at all closely related. As may be seen from Figure 20 the skull is that of a rhachitome in diagnostic features, and (except that the face is not so expanded) comparable to that of *Edops*. As in that genus, there is a well developed intertemporal. The lacrimal is more primitive than that of *Edops* in extending posteriorly toward or to the orbit. On the other hand, Jaekel does not figure a septomaxilla; but it may well be that this was present but not distinguished by Jaekel from the anterior end of the lacrimal.

If this skull be compared with the material of *Capetus*, *Nyrania* and *Gaudrya*, all described from Nýřany, it appears that all of them are probably generically identical with Jaekel's specimen. *Capetus palustris* was founded by Steen (1938, pp. 241–242) on the basis of a large skull table, previously undescribed, and a second skull which had been erroneously identified by Broili (1908, pl. 1, fig. 1) as *Sclerocephalus*. Broili's specimen strongly suggests both Jaekel's and *Edops* in its general configuration and sculpture pattern; Steen's specimen, except for a somewhat greater projection in the tabular region, is closely comparable to Jaekel's and indeed, is even closer in some regards to the *Edops* skull table.

Nyrania trachystoma was founded on two skulls, described by Fritsch (1901 [1889], vol. 2, pp. 33–36, figs. 138–139; pl. 62, figs. 1, 2; pl. 63, figs. 1–6; cf. Steen 1938, p. 242, fig. 28); no postcranial remains are known. One of the skulls, as noted later in this paper, is probably a specimen of *Cochleosaurus*; the other (Fritsch, pl. 62, fig. 1) was the first described and may be designated as the holotype. It shows the roofing elements excellently. The general contours and sutural pattern in the temporal region are almost exactly those seen in *Capetus*, Jaekel's specimen, and *Edops*. The only exception is that the single tabular preserved appears to show a lateral projection; however, this may well be an accident of preservation. Steen gives a restoration of the skull roof which is said to be derived from the electrotype of this skull (the original is not preserved). However I find the pattern given by her in the temporal region difficult to derive from the electrotype available to me, and markedly different from that of the specimens previously described in this section.

A small part of the palate can be seen on this last specimen (Steen's restoration of the "*Nyrania*" palate is mainly based on the specimen which I regard as *Cochleosaurus*.). Palatine and ectopterygoid fang

pairs are visible; the posterior margin of a naris indicates that the choanae were, in typical rhachitome fashion, laterally placed and widely separated from each other. Part of the palatine and vomer are preserved, and show a denticulation and, particularly, a radiate striation similarly seen on the *Edops* palate. The nature of the palatal surface appears to have been the reason of the appropriate assignment to "*Nyrania*" of an isolated vomer and a pterygoid (Fritsch, pl. 62, figs. 3–6)[1]. If the pterygoid be compared with that of *Edops*, their almost exact identity will be noticed; in fact, the only difference is that the medial margin of the palatal ramus (the lower part of the right margin in Fritsch's figure) is straighter than in *Edops*, indicating a still smaller interpterygoid vacuity.

Gaudrya latistoma (Fritsch 1901, pl. 61, fig. 1) has as a type an imperfectly preserved snout which shows the palate from above. The marginal teeth are seen in the premaxillary region, with much the arrangement of "*Nyrania*". The vomers are in part represented by bone; the remainder of these elements, part of the pterygoids, and the palatal aspect of the premaxillae are represented by impressions of their ventral surface. The arrangement, denticulation and striation of the structures present is comparable to "*Nyrania*" and *Edops*, and it seems safe to assume that the *Gaudrya* type specimen is a snout of "*Nyrania*" — over which, however, it has technical priority in description. Especially notable is the long median suture between vomers and (presumably) pterygoids, confirming the evidence of the supposed "*Nyrania*" pterygoid that the interpterygoid vacuity was very small. It seems reasonably certain that, except for this last point, the *Gaudrya* [=*Nyrania*, *Capetus*] palate was very similar to that of *Edops*; but in view of the incomplete nature of the material I have not attempted to figure a restoration.

With *Gaudrya* and "*Nyrania*" Fritsch associated various other materials, including jaws, a typical rhachitome ilium, etc., but there is no proof of association.

Gaudrya, as described above, is without question a close relative of *Edops*; the only known point of distinction is that the facial region of the American genus is more expanded — a feature associated perhaps with its greater size. The two genera may possibly be identical; in any event *Gaudrya*, as the older form, may reasonably have been ancestral to the Texas genus.

[1]The "Gaumenknocken von fraglicher Natur" shown with the pterygoid is a *Diplovertebron* pelvis.

Leptophractus

(Fig. 20)

A still earlier member of the *Edops-Gaudrya* group of primitive rhachitomes is *Leptophractus obsoletus* of the Westphalian cannel coal at Linton, Ohio, redescribed by the writer (1930, pp. 126–130, figs. 23, 24); this is represented by several fragmentary specimens of the skull of a large amphibian, with a pitted sculpture similar to that of *Edops*. The facial region of the skull is but moderately elongated; the lacrimal is more primitive than that of either of the two genera described above in retaining a broad orbital contact. Posteriorly there can be seen a well developed otic notch with rounded margins and with cheek and table firmly fused anterior to it. An intertemporal is present. The posterior portion of the table is, unfortunately, not preserved so that the shape and connections of the tabular, important in diagnosis, cannot be determined.

The marginal teeth are short but very stout and close-set. The anterior part of the palate is visible in one specimen. The internal nares are widely separated, in rhachitome fashion, by broad vomers with fang-pairs anterior to the nares. A similar tusk pair is seen on the palatine. There is a median suture of the pterygoid elements extending well behind the level of the nares; this condition, together with a view of a part of the palate seen from the dorsal surface through the orbit, indicates that palatal vacuities were present, but small, and suggests that (as expected) the basal articulation was movable. The jaw is incompletely known.

In my description in 1930 I assigned this form to the Embolomeri, partly because of the presence of primitive features not ordinarily found in rhachitomes, partly because of the assumption then prevalent that large Carboniferous labyrinthodonts were *ipso facto* embolomeres. Reconsideration in the light of our present knowledge leads to a different conclusion. The type of otic notch, fusion of cheek and table and, particularly, the structure of the vomerine region, show that this form is a primitive rhachitome closely allied to *Edops* and *Gaudrya*.

No postcranial remains are associated. As I noted in 1930, it is highly probable that the specimen described by Cope as *Ichthyacanthus platypus* and figured by Moodie (1916, pl. 23, fig. 1) belongs to the same genus, although the specimen is of rather modest size for the known skull material. Part of the column and the hind leg are present. The vertebral structure is, unfortunately, obscure. The hind leg, including a nearly complete foot, is very similar to that of *Eryops*.

As noted elsewhere, I was in error in my earlier inclusion of *Erpetosuchus kansensis* in this genus; this form is a true embolomere.

Lusor

(Fig. 25)

I note here, with considerable hesitation, the single skull roof from the Lower Permian of Ruprechtice (Ruppersdorf) Bohemia, described by Steen (1938, pp. 249–250, fig. 35) as the type of *L. tenellus*. This is in many regards a normally-built rhachitome. As far as the preorbital and cheek regions are concerned, *Lusor* could well be either a primitive rhachitome of the *Edops* type or a more advanced *Eryops*-like form; unfortunately occiput and palate, which show most of the key features, are not present. However the skull table, as preserved and figured, is seemingly very abnormal. As described, it is exceedingly short; far shorter in relation to the length of the suspensorial region than in any labyrinthodont ever described. In the lateral series of table elements, Steen believes the intertemporal to be absent, the supratemporal to be a small element lying between postorbital and parietal, and a small element medial to the squamosal to be the tabular. There is, in this interpretation, almost no otic notch, and a further un-rhachitomous feature is that the tabular reaches forward to make a contact with the parietal.

An alternative interpretation suggests itself. It is obvious from Steen's figure that the posterior margin of the table is imperfect. If we assume that the posterior section has been lost, we may restore the skull in very different fashion. The supposed abnormal supratemporal becomes a normal intertemporal; the supposed tabular is part of the supratemporal; the true tabulars and postparietals, when restored at the back of the skull, complete a structure highly comparable to the contemporary American *Edops* or to earlier Bohemian members of the same group.

A form also from Ruprechtice which at first sight appears to contrast markedly with *Lusor* is *"Sclerocephalus" credneri* (Fritsch 1901, vol. 4, p. 93, fig. 392; Steen 1938, pp. 247–248, fig. 33). Only one specimen is known; as Steen notes, other material assigned to this species by Fritsch and Broili does not pertain. The specimen includes the skull and anterior half of the body. The details of the postcranial skeleton are not well preserved, but the structure appears to be in general that of a rhachitome. The dermal shoulder girdle shows a

capping cleithrum and well expanded clavicles and interclavicle; the last is relatively short and broad, in contrast with this element in the local contemporary *Chelydosaurus*.

Most of the skull roof is preserved. As was said, the contrast with *Lusor* is at first sight great, for this form appears to have a sharply pointed snout, as compared to the broadly rounded *Lusor* muzzle. But it is obvious that this is due to post-mortem crushing and folding. If Steen's figures of the two forms (her figs. 33 and 35) be compared, it will be noted that not only in the marked jaw elongation but in various details of skull pattern the two are identical, and it seems reasonable to conclude that these local contemporaries are generically if not specifically identical.

Unfortunately, as Steen notes, the posterior portion of the skull table is incomplete posteriorly, as in the *Lusor* type. This defect is partially compensated in a third Ruppersdorf specimen, assigned by Fritsch (1901, pl. 57, fig. 1) to *Chelydosaurus vranii* but apparently belonging to the present form. This shows the posterior part of a skull and jaw fragments. An intertemporal is present as in the specimens already described, and a supratemporal which, on the left side of the specimen, shows a configuration comparable to that of the right side of "*Sclerocephalus credneri*". In this form the true tabular is present on the right side, but the actual posterior margin of the table is imperfect.

Dendrerpeton

(Figs. 4, 13, 21)

D. acadianum is a small amphibian, described by Owen (1853) and Dawson (1882 etc.) in various papers and recently reviewed by Steen (1934, pp. 468–479); it was the commonest inhabitant of the hollow tree stumps in the typical Westphalian Coal Measures of the Joggins, N. S. There exist numerous skulls and a considerable amount of postcranial material, the association of which with the skulls is not always certain.

The small skull, as restored by Steen, is relatively high and narrow, in primitive fashion, with steeply sloping cheeks. In connection with the taxonomy of Joggins rhachitomes, one may call attention to the fact that skulls recognized as belonging to this species (Steen 1934, figs. 10, 11) vary considerably in pattern. The face is rather short, the table relatively long. The roofing pattern is definitely

rhachitomous in nature and in various features, including the significant presence of an intertemporal, resembles that of the preceding genera. The snout, as in those genera, is broad. The lacrimal is restored by Steen as running from naris to orbit, but the evidence of its reaching the latter opening does not appear conclusive. The otic notch is very prominent, and is overhung by the tabular, suggesting the initiation of a trematopsid or dissorophid tendency toward otic notch closure.

In the palate the nares are large, a feature perhaps associated here with relatively small absolute size. The large vomers and widely separated choanae are typically rhachitomous. No tooth-pair is described on the vomer; the primitive single pairs are found on palatine and ectopterygoid. The palatal vacuities are more advanced than

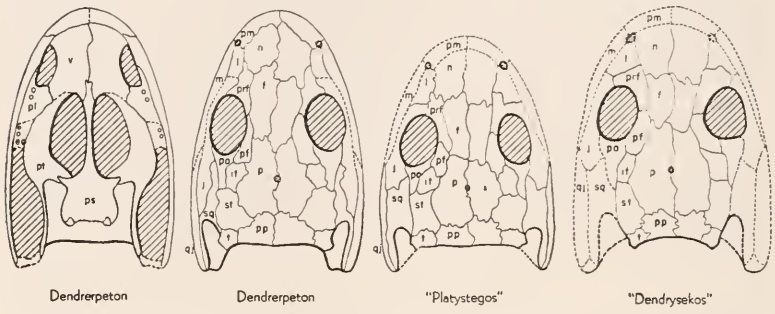

Fig. 21. Dendrerpetonts from the Joggins. After Steen.

those of *Edops* — they are larger, and rounded anteriorly; the two pterygoids have lost their contact with each other, and the anterior margins of the vacuities are formed by the vomers, with the parasphenoid wedged between them. On the whole, the condition is approximately that seen in *Eryops*. However, despite this enlargement of the vacuities the basal articulation, at the posterior margin, of palate with braincase is persistently mobile. Steen notes that (as in *Edops*) the supraoccipital region was cartilaginous, although the otic region was well ossified; a twelfth nerve was present; and, as in *Edops*, the occipital condyle is a persistently single structure, carried by basioccipital as well as exoccipitals.

No vertebrae are known in the case of the Carboniferous genera described earlier in this section, and their rhachitomous nature, while probable, is incapable of direct proof. Steen describes rhachitomous

vertebrae associated with *Dendrerpeton*. There are present neural arches and various central elements. Certain of the central structures are definitely intercentra of large size, hemicylinders U-shaped in end view. Steen believes the pleurocentra to have been equally large and to have formed complete rings, and so restores the column (her fig. 5 D), suggesting that this is a reduction stage from an embolomerous condition (p. 499). As will be noted from her description, however, there is no evidence for such pleurocentra from associated material, but merely from "a vertebra of very similar type" (cf. *infra*, *Dendryazousa*). A more normal rhachitomous structure may well have been present.

Considerable limb material is reasonably associated by Steen. The shoulder girdle is similar to that of *Eryops*; the presence in the humerus of an entepicondylar foramen, rare in amphibians, is noteworthy. The pelvis is well ossified; the ilium has a posterior development lost in typical rhachitomes; the nature of the dorsal expansion or process is uncertain.

Dendrerpeton is definitely a primitive type of rhachitome, and the oldest form which can be certainly assigned to the group on the positive basis of vertebral structure. It is, nevertheless, more advanced in certain regards than later genera, such as *Edops*. It is possible that it lay rather to one side of the main line of rhachitome development and might have lead, by parallel evolution, to some of the members of the Permian rhachitome assemblage. A further point to be kept in mind is that, because of the peculiar conditions under which the Joggins fauna is preserved, *Dendrerpeton* may be a young form of some relatively large adult type.

Several other Joggins genera have been erected on materials very similar to those of *Dendrerpeton*, and are very probably congeneric. *Dendrysekos helogenes* (Fig. 21)[1] was described by Steen (1934, pp. 481–482, fig. 14) on the basis of a skull table referred by Dawson to *Dendrerpeton*. It differs in the more slender proportions of the table combined with relatively short frontals, but otherwise is, as far as known, very similar to *Dendrerpeton*. *Platystegos loricatum* (Fig. 21) was described by Dawson but not figured; Steen (1934, pp. 480–481, figs. 12, 13) has redescribed and figured the skull material which represents this Joggins amphibian. As Steen notes, the skull pattern is practically indistinguishable from that of *Dendrerpeton*. The generic

[1]In the restoration of *Dendrysekos*, as in several other cases, I have omitted the occipital aspect of the posterior table elements, although they are visible in the figures of the flattened skull.

differences are supposed to lie in the much flatter contours of the *Platystegos* skull. There is, however, no published evidence (such as a control through measurement of palatal width) to show that the flattening is not post-mortem. In my figure I have, for better comparison, placed the *Platystegos* cheeks in the same position as those of *Dendrerpeton*, with which one may suspect it is generically identical.

Dendryazousa was established by Steen (1934, pp. 482–484, figs. 15–17) on the basis of a single slab from the Joggins exhibiting remains of a skull and postcranial elements. The skull table, with small tabulars which do not reach the parietals, is clearly that of a rhachitome of some sort. In most regards the skull roof, as far as preserved, is similar to that of the last three genera named; the evidence suggests that the tabular was pointed rather than blunt-tipped. However, there are specimens, such as those described by Steen as R 4554, R 4553 (one of three skulls), which are assigned to *Dendrerpeton* by her and yet are nearly as pointed in the tabular region.

With *Dendryazousa* Steen associates the other structures found on the slab with the skull, including clavicles, a femur and a pelvis which, as far as preserved, might be embolomerous, seymouriamorphan or even reptilian in nature. Of particular interest are disarticulated vertebrae present on the slab. As Steen notes, there appear to have been intercentra and pleurocentra subequal in size, both extending from the ventral surface to the neural arch. The appearance of the vertebrae, as restored, is thus embolomerous. Steen, however, notes that when seen in section some elements (presumed pleurocentra) are complete rings, others (?intercentra) are incomplete dorsally. This is the type of vertebra seen in the primitive seymouriamorph *Discosauriscus*, and one which it is difficult to believe was associated with a rhachitomous skull. It is notorious that Joggins slabs may show juxtaposition of a variety of materials quite unrelated to each other. The vertebrae seen in section are far removed on the slab from the skull. One may reasonably suspect that the "association" here is accidental and that these vertebrae belong to some other animal, such as *Calligenethlon* (q.v.)

In conclusion, one may say of the Joggins material discussed above, that there is adequate evidence of the presence of a single genus of primitive rhachitome, *Dendrerpeton*, but that in consideration of the acknowledged variation seen in that species, further evidence is needed to afford proof of the separate identity of *Dendrysekos*, *Platystegos* and *Dendryazousa*.

Cochleosaurus

(Fig. 20)

The forms discussed above appear to be both primitive and generalized ancestral rhachitomes. There are, in addition, various genrea, mainly late Carboniferous in age, which exhibit similar features but appear to be in some degree specialized or advanced. Clues to their identification lie, as we have seen, in all, or most of these features: presence of an intertemporal; small interpterygoid vacuities; movable basal articulation; single occipital condyle.

Cochleosaurus bohemicus of Nýřany is a form somewhat advanced in nature, but still persistently primitive in certain respects. It was first described by Fritsch (1901, vol. 2, pp. 30–31, pl. 60, fig. 1–3; vol. 4, p. 92, fig. 391); other material was described by Broili (1905) and Stehlik (1924, pp. 277–278, fig. 10); Steen, in reviewing the species (1938, pp. 243–246, figs. 29–32), notes that still other material, described by Fritsch as *C. falax*, *Dendrerpeton pyriticum* and *D.* ? *deprivatum* (Fritsch 1901, vol. 1, p. 71; vol. 2, pp. 6–8, 31, figs. 126–127, pls. 49, figs. 1–9; 50, figs. 1–4, 60, fig. 4), also belongs to this form; and I have noted above that a supposed second specimen of "*Nyrania*" (Fritsch, pl. 63, figs. 1–6) belongs here.

The general outlines of the *Cochleosaurus* skull are similar to those of generalized types, such as the contemporary *Gaudrya*, except that the snout is rather narrow, and that during ontogeny characteristic dermal lappets appear on the postparietals. The intertemporal is retained; the lacrimal barely fails to reach the orbital margin. A feature noted by Steen is the tendency for reduction and loss of the pineal opening in large individuals. The palate is of a typical rhachitomous pattern. A primitive feature is the retention of a movable basal articulation (see especially Fritsch, pl. 50, fig. 1 for this region of the pterygoid). The interpterygoid vacuities, as restored by Steen, have developed in size to the typical rhachitomous condition seen in *Eryops*. However the specimen shown on pl. 63, fig. 2 of Fritsch's work indicates that the pterygoids were broader than in her restoration and the vacuities less developed. A marked advance appears in the structure of the occipital condyle. In other rhachitomes exhibiting such primitive features the condyle, where known, is single; in *Cochleosaurus*, a specimen figured by Broili (1905, pl. 2, fig. 3) appears to show a distinctly double condyle comparable to that seen in very advanced rhachitomes or stereospondyls. There is no certain evidence as to postcranial structures.

The curious combination of primitive and advanced features exhibited by *Cochleosaurus* is an example of the parallelism in phylogenetic development which appears to have occurred in labyrinthodont evolution, and which makes so difficult the determination of their true relationships and classification.

Eugyrinus

(Fig. 22)

With this genus we enter on the discussion of a series of short-faced rhachitomes, mainly of small size and for the most part Pennsylvanian in age. They all exhibit primitive features to a greater or lesser degree.

Eugyrinus wildi is founded on a small skeleton from early Pennsylvanian Coal Measures at Colne, Lancashire. First briefly described by Smith Woodward in 1891 (as "*Hylonomus*"), it has been more adequately studied by Watson (1921; 1940, pp. 214–217, figs. 12–15). A second skull from this locality was mentioned by Bolton (1904, p. 406), but has received no further notice. The skull is short — particularly, short faced — and, as might be expected in a small form, the orbits are large. As in certain other forms with large orbits, the jugals do not extend forward beneath them. The general roofing pattern is that of the rhachitomes, including tabulars of small size. The lacrimal reaches the orbit in primitive fashion (a feature correlated, as well, with the short face) and, much as in *Edops*, there is a surface exposure of the septomaxilla. The supratemporal is large, and the intertemporal is retained. As far as it is preserved, the palatal construction is of the general rhachitomous type, with broad vomers. The interpterygoid vacuities are of very large size. The nature of the basal articulation is not stated; Watson's original figure suggests motility. The quadratojugal extends inward to enter the jaw articulation to an unusual degree. In contrast with most early labyrinthodonts, the articular region is somewhat in advance of the level of the occiput. The basal area of the parasphenoid is moderately expanded. The carotids entered its substance well posteriorly, as in *Edops*. The jaw is of a typical labyrinthodont and, more specifically, of a rhachitomous type, with a well developed coronoid elevation and a moderate retroarticular process. The braincase was feebly ossified; the presence of a well-preserved basioccipital is strong evidence that the condyle was persistently single.

Much of the posteranial skeleton and armor is present. In the vertebral column, including about 26 presacrals, the neural arches are visible, but there is no evidence regarding central elements. The dermal shoulder girdle and pelvis are rhachitomous in pattern; the pubis, as in young individuals or advanced forms, was unossified.

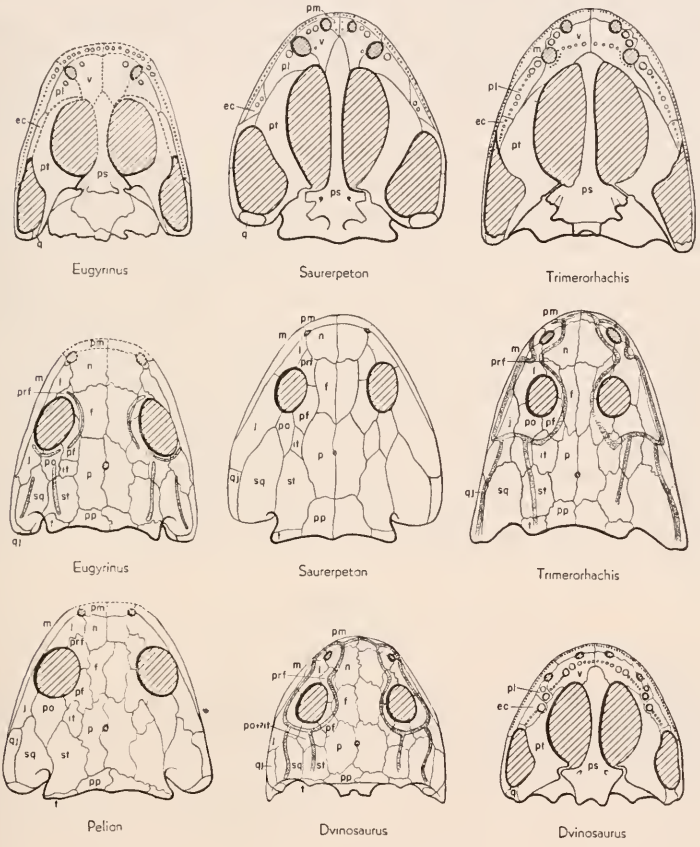

Fig. 22. Short-faced edopsoids. *Eugyrinus* after Watson; *Saurerpeton* after Steen, Romer; *Trimerorhachis* after Case; *Dvinosaurus* after Bystrow.

Except that it is more primitive in certain features, the skull shows great similarity to that of the common "*Branchiosaurus*" of the Permian,

and Watson therefore concluded that it was a member of the supposed phyllospondyl group, of which "*Branchiosaurus*" was typical. In such features as the large interpterygoid vacuities, *Eugyrinus* was far more advanced than the characteristic large labyrinthodonts of the period (embolomeres, loxommids), suggesting to Watson that the branchiosaurs had evolved in a fashion similar to the labyrinthodonts, but as a parallelism, and at a much faster tempo.[1]

However, as I have pointed out elsewhere (1939a), "*Branchiosaurus*" is the young form of a typical rhachitome of the early Permian, and the supposed order Phyllospondyli is non-existent. The resemblances of *Eugyrinus* to "*Branchiosaurus*" are due merely to the presence of rhachitomous features as seen in small or young members of that group. *Eugyrinus* may be an adult, but it seems probable that it is a young individual of a form which as an adult belonged to the *Edops-Leptophractus-Gaudrya* group. No large specimen of this sort is known from this stage of the English Coal Measures but in view of the general paucity of skull remains, this is not surprising. The major differences between *Eugyrinus* and an *Edops*-like rhachitome have to do with the great elongation of the face in the large form, the greater development and posterior position of the suspensorial region, and the much smaller palatal vacuities of the *Edops* type. These are, exactly, the main changes seen in the ontogenetic development of "*Branchiosaurus*" into the adult *Onchiodon*; they strengthen our belief in the identification of *Eugyrinus* as a young, although probably post-larval, member of the primitive rhachitome group.

Pelion

(Fig. 22)

Pelion lyelli was the first amphibian described from the Upper Westphalian Cannel of Linton, Ohio; it has been best figured by Moodie (1916, pl. 24, fig. 1). Somewhat obscured by a film of matrix, it exhibits the under surface of the skull and jaws, and part of the limbs and vertebral column of a small amphibian; the girdles, ribs, and squamation are not preserved. The form is obviously very short-headed, and in its outlines and in what can be seen of the palate is very similar to *Eugyrinus*. The limbs are rather well developed, but

[1]It was primarily as a result of this suggestion that the writer (1930) and Steen (1931), when confronted, in the Linton fauna, with various amphibians with an "advanced" palatal structure, assigned them to the Phyllospondyli; whereas they now appear to be properly assignable in part to the rhachitomes, in part to the ichthyostegals.

detail is obscure. It now appears that the skull which I redescribed in 1930 (pp. 98–100, fig. 7) as *Branchiosauravus tabulatus*, as well as a second specimen figured there for the first time, is generically and probably specifically identical with *Pelion lyelli*. I had formerly believed *Pelion* to represent a somewhat different sort of Linton amphibian (here described as *Saurerpeton*) because the limbs of the *Pelion* type were quite different from those of a postcranial skeleton which I then thought to belong to "*Branchiosauravus*". It appears, however, that this identification was incorrect; the contours of the skull of my supposed new genus agree well with those of *Pelion* and differ considerably in proportions from that described below as *Saurerpeton*.

It is quite possible that a number of other small and poorly preserved types — *Tuditanus sculptilis*, *T. walcotti*, *Erpetosaurus minutus* — from Linton and the neighboring locality (slightly earlier stratigraphically) at Cannelton (Moodie 1916 etc.) are identical with *Pelion*, but they may be immature individuals of labyrinthodonts of other sorts.

If the skull roof of *Pelion* be compared with that of *Eugyrinus*, it will be seen that in almost every feature of pattern and proportion the two are practically identical; detailed description of these features is unnecessary. We may note, however, that the supratemporal is still larger, the tabular still smaller, than in *Eugyrinus*, and there does not appear to be the postero-medial development of the quadratojugal seen in that genus. The palate is imperfectly known, but there appears to have been a movable basal articulation; the anterior ramus of the pterygoid was apparently broader and the size of the interpterygoid vacuities must have been, in consequence, rather smaller than in *Eugyrinus*. The condyle was apparently single.

In the case of the English genus, no large form is present to which *Eugyrinus* might be assigned as a "baby" individual. At Linton, however, we have, in *Leptophractus*, a large mature form into which the tiny *Pelion* might have grown. As noted previously, the differences are great, but of exactly the sort bridged in the development of "*Branchiosaurus*" into *Onchiodon*.

Erpetocephalus

This genus is based on a skull (*E. rugosus*) described by Huxley (1867, pp. 368–69, pl. 23, fig. 2) from Jarrow in the Leinster Coalfield of Ireland. Apart from traces of the shoulder girdle, we know only

the dorsal surface of the head in this specimen. The skull is, as in the last two genera, small (the length about 65 mm.), and the proportions — with a very short face, moderately developed table and well-incised otic notches — are comparable to those of *Eugyrinus* and *Pelion*. Unfortunately, however, sutures are not determined, and the position of the genus must remain problematical unless further material be identified and adequately described.[1]

Lydekker (1890, pp. 169–170) believed that this skull pertained to the body skeleton of the elongate embolomerous amphibian from Jarrow, described by Huxley as *Ichthyerpeton*, and states that two specimens in the British Museum from that Irish locality show skulls similar to that of the *Erpetocephalus* type; I am not familiar with this material. In 1891 Lydekker described another skull from Jarrow, belonging to the Dublin Museum. This was a short-headed form obviously similar in general contours to *Erpetocephalus*; Lydekker, however, assigned it to "*Ichthyerpetum*" (*I. hibernicum*). Lydekker further compares the *Erpetocephalus* cranial material with *Pholidogaster*.

These various assumptions of Lydekker, who was notoriously an over-zealous "lumper" of fossil material, cannot be taken seriously without further investigation. Those who have worked with coal measures material are aware how easy it is to make improper identifications of cranial roof material. It would be most unusual to find a short, broad skull of the *Erpetocephalus* type in association with the obviously elongate and rather eel-like body of *Ichthyerpeton* and there is no resemblance between the *Erpetocephalus* skull and that of *Pholidogaster*, as described by Watson.

Micrerpeton and other Mazon Creek "Larvae"

The nodule bed of the Pennsylvanian of Mazon Creek, Illinois, and the adjacent region has yielded but few amphibian specimens, most of them described by Moodie (1912 etc.). Of these, one (*Spondylerpeton*) is a fragment of an embolomere of considerable size; *Amphibamus* and *Miobatrachus* represent a special group; *Erpetobrachium* exhibits indeterminate small limb bones. The other specimens consist of the remains of small amphibians which were encased completely (or nearly so) in the nodules. These have been described as: *Micrerpe-*

[1]The nature of the material at the postero-lateral corner of the skull is not too clear. Possibly the jaw articulation was placed well back of the posterior margin of the skull table, in which case there appears an interesting resemblance to the amphibamids.

ton caudatum, Eumicrerpeton parvum, Mazonerpeton longicaudatum, M. costatum, Erierpeton branchialis, Cephalerpeton ventriarmatum and *"Amphibamus" thoracatus.* This material was described and figured by Moodie in various early papers and again in his monograph of 1916 (particularly pp. 51–66, 131–134, pls. 2–5). It is very probable that these names and specimens represent the larvae and young of one or more primitive rhachitomes, of which the adults, owing to the type of preservation at this locality, are unknown. Many of these forms were classed by Moodie among the "branchiosaurs", an identification which today strongly suggests immaturity of the individuals concerned. In none is there any evidence of the skull or body elongation characteristic of the better known embolomeres, but it is, however, possible that certain of them may be immature specimens of the amphibamids known from this bed, or of the ichthyostegals, which must have been present in North America at the time although unrecognized at Mazon Creek. *Eumicrerpeton* is known from two tiny animals an inch or so in length, which show a body outline, impressions of the intestine, but few traces of the skeleton. The head impression shows that the form was, as expected, short-skulled and, particularly, short-faced. *Erierpeton,* somewhat larger, shows a few body impressions and the skull outlines, together with pterygoid flange impressions, of a little animal which might be comparable to the *Eugyrinus-Pelion* type. *"Amphibamus" thoracatus* is a poor specimen of approximately the same size as the last; it exhibits a skull outline (but one, apparently, with a relatively slender shape) and a few postcranial elements. A further stage in size increase is seen in *Micrerpeton,* the type of which is a delicately preserved entire body. The general proportions of the skull and body and of such ossifications as are apparent are of the typically "branchiosaurian" type expected in a young rhachitome; it will be noted that the trunk, with some 20–25 presacrals, is of a rather compact and typically rhachitomous build, rather than the more slender and more sinuous build of the characteristic embolomeres. *Micrerpeton* had a length to the pelvis of about 3 cm., a total length of about 5 cm. Still larger are *Mazonerpeton longicaudatum* and *M. costatum.* The former is a nearly complete skeleton, measuring about 6 cm. to the sacral region, poorly preserved as to detail but seemingly rather comparable to *Micrerpeton*; the latter, somewhat larger, includes partially disarticulated remains of the column and, apparently, a shoulder girdle. Of this series of skeletons the "giant" is *Cephalerpeton ventriarmatum,* which may have been about 10 cm. long to the pelvis and have had

a total estimated length of perhaps 17 cm. Much of the presacral skeleton is present, but little detail of morphological interest has been observed.

Saurerpeton

(Fig. 22)

S. obtusum appears to be the proper name for a Linton amphibian which I assigned in 1930 (pp. 94–98, figs. 4–6) to *Pelion lyelli* in error (*cf. supra*); in this I was followed by Steen (1931, pp. 869–874, figs. 15, 16). This material was originally described as *Dendrerpeton* (later *Tuditanus*, *Erpetosaurus*) *obtusum* and *Sauropleura latithorax*; *Saurerpeton* was based by Moodie on the latter form.

Two of the *Saurerpeton* skulls are about 65 mm. long; a third (that described by Miss Steen) about one-third this length. The sculpture is strongly developed on the skull roof. The pattern of dermal elements is clearly that of a primitive rhachitome, and there are close comparisons with *Pelion* and *Eugyrinus* in many regards, such as the long lacrimal, tiny tabulars, lack of posterior development of the suspensorial region, and (especially) the very short face. This last feature, characteristic of larval or immature individuals of other genera, suggests that we are here dealing likewise with immature (i.e., "branchiosaur") material. Against this conclusion, however, is the most distinctive feature of the *Saurerpeton* skull — the great elongation of the post-orbital region, in which parietal, supratemporal, jugal, squamosal and even the postparietal are involved. Apart from the ichthyostegals (in which it appears to be a truly primitive feature) post-orbital elongation is rare in Paleozoic labyrinthodonts and indicates that, young or old, the *Saurerpeton* material represents a specialized development.

The palate shows distinctive features. The marginal teeth are tiny and numerous. In contrast with the forms considered earlier in this section, a pair of anterior vacuities, presumably for lower jaw tusks, is present in the palate, between premaxillae and vomers.[1] There are well developed fang-pairs on vomer, palatine and ectopterygoid, and there are some indications of the development of additional small teeth on these elements as well as on the pterygoid. The interpterygoid vacuities are large. The parasphenoid seems to have extended well forward between the vomers, and was rather more flattened in the region of the cultriform process. The posterior end of

[1]Due to the imperfect nature of her specimen, Miss Steen appears to have confused this vacuity with the choana.

the bone was rather well expanded in the basisphenoid region (there are carotid foramina) but constricts posteriorly, suggesting the primitive monocondylar condition. The shortness of the jaw is shown by the abbreviate nature of the quadrate ramus of the pterygoid.

The *S. latithorax* type (Moodie 1916, pl. 17) gives our only data on the postcranial skeleton. This specimen shows the clavicle and interclavicle from the dorsal aspect. As may be seen from Moodie's figures, these elements were very greatly expanded ventrally, their degree of development being comparable to that of the Permian rhachitome *Trimerorhachis*. This breadth of the dermal shoulder elements appears to confirm the evidence from the skull that the head and trunk of *Saurerpeton* were of a broad, flattened type. Most of the anterior appendages are preserved, including a partial foot; they were relatively feeble. Part of the ventral squamation is shown, and a number of ribs, but the vertebrae are unknown.

The flattened body and small limbs strongly suggest that *Saurerpeton* was already advancing in the neotenic type of development which was to become a dominant feature of later labyrinthodont evolution. The facial abbreviation might be regarded as a larval feature; however, the elongation of the post-orbital region is a definite and characteristic specialization which we shall see repeated in certain later rhachitomes and stereospondyls.

Trimerorhachis

(Figs. 10, 12, 13, 22)

This genus is one of the most common fossils in the early Permian redbeds of the Texas region. Its presence in the lower formations of the Wichita group is uncertain, but in the Admiral and Belle Plains formations it is very abundant, and it is not uncommon in the Clear Fork. Apart from the type, *T. insignis*, some seven species have been named; for the most part, however, specific distinctions are none too clear and some of these species are rather doubtfully members of this genus; revision is badly needed. A comprehensive anatomical account has most recently been given by Case (1935; see also Case 1911, pp. 39–47, 106–112, pl. 12; Broom 1913, pp. 569–578, figs. 4–10; Williston 1915, 1916); a study of the braincase by Wilson has been interrupted by the war.

Trimerorhachis was, for the Permian, a form of modest size, with a skull but a few inches in length. It exhibits a curious combination

of advanced and primitive characters. Its general habitus is that of a Triassic stereospondyl. The skull was broad and flat, and the postcranial skeleton indicates a similar breadth and flattening of the body. The limbs were tiny, and obviously were unable to support the body to any degree for land locomotion. Obviously *Trimerorhachis* was a water-dweller, a conclusion confirmed by the presence of well defined lateral line grooves on the skull; the description by Case of ossified branchial elements indicates that the animal was a gill breather. We have here an early instance of the neotenic tendencies shown in many amphibians of later geologic and recent times.

The skull roof pattern is of a primitive rhachitomous type, preserving the intertemporal, and with the lacrimal reaching orbit and naris. It is, however, of a specialized nature in that the orbits are far forward, the table and cheeks greatly elongated. This pattern is almost exactly that seen in *Saurerpeton* and suggests that *Trimerorhachis* is a descendant of that Carboniferous form. The otic notch, still developed in *Saurerpeton*, is here, however, represented only by a slight indentation, and a very exceptional feature of *Trimerorhachis* is the extension of both lacrimal and postorbital below the orbit so as to exclude the jugal from the orbital margin.

The palate is also basically similar to that of *Saurerpeton*. There are interpterygoid vacuities of considerable size, although the pterygoids extend well forward. The cultriform process of the parasphenoid is flattened, the body of the bone moderately expanded, with the carotids apparently passing forward in the substance of the bone. As in *Saurerpeton* there are small anterior palatine fenestrae. Also as in that genus the lateral teeth are very small and very numerous. The palatal teeth show a development of the type seen in most temnospondyls of the later Permian and the Triassic. On the vomer there is found the customary pair of fangs, but in addition there is a transverse series of teeth between the two choanae and a festoon of small teeth along the inner border of each choana. On the palatine there persists a large tooth pair, but behind this there is a long series of smaller teeth running the length of that bone and the ectopterygoid. (In *Saurerpeton* the palate is poorly known, and it is possible that a similar dentition may have been in process of development.) *Trimerorhachis* appears to have retained a movable basal articulation of palate and braincase.

No epipterygoid is known. On its medial, articular face the pterygoid bears a pit, a "conical recess" which presumably received the basipterygoid process of the basisphenoid.

Reduction of endochondral bone, characteristic of advanced types, is well under way. There is an ossified sphenethmoid, but this is separated by an unossified gap from more posterior elements. The basisphenoid is represented by a film of bone in the region of the pituitary fossa and the base of the basipterygoid process, noted by Case and faintly shown in his figure 5 (1935). The basipterygoid process itself was unossified, but its anterior and posterior margins are defined by prominent ridges, well shown in Case's figure. No prootic has been described, and the opisthotics are feebly ossified. On the other hand, the basioccipital persists and the exoccipitals are large elements, although only an unossified gap represents the supraoccipital region. The exoccipitals extend upward to the skull roof, and ventrally extend inward, in typical fashion, on the floor of the medullary region. Although the exoccipitals are prominent at the margins of the condyle, they are still connected by the well ossified basioccipital ventrally and hence the condyle is essentially still a single structure.[1]

The jaw is well preserved, and shows diagrammatically the generalized primitive structure. The two posterior members of the coronoid series are heavily denticulated; there is a modest retroarticular process.

In the vertebral column the neural arches are low, as might be expected in a form both small in size and flattened in contours. The pleurocentra are considerably reduced. The intercentra, on the other hand, although ossified only superficially, reach upward to a broad contact with the neural arches, in anticipation (so to speak) of the stereospondylous condition.

The clavicle and interclavicle are very broadly expanded ventrally. The scapulocoracoid is a single element, incompletely ossified both dorsally and ventrally. In the pelvis, the pubis is, as in advanced amphibians generally, unossified. The ilium as preserved, is a slender ascending structure without any dorsal expansion or sign of sacral attachment; it is, however, possible that the dorsal cartilaginous continuation of the bone may have been developed in *Eryops*-like fashion. The limbs are small and poorly ossified. Humerus and femur are built on a plan markedly different from that of the contemporary *Eryops*. The humerus is relatively long, with a developed shaft region, and with the planes of the two ends "twisted" not more than 30 degrees or so. The delto-pectoral crest is situated nearly half

[1]Case's figure of the occiput minimizes the importance of the basioccipital in the condyle; see, rather, Williston 1915, fig. 5, I.

way down the bone, and while rugose, has little ventral projection. A flange of bone connects the crest distally with the feebly developed supinator process. In the femur, the internal trochanter is developed as a stout ridge; the outer (posterior) limb of the ventral trochanteric system is absent; the fourth trochanter is moderately developed and rugose, but the ridge distal to it (linea aspera, adductor crest) is low and rapidly dies out. The ectepicondyle is powerfully developed. Case has reasonably restored the front and hind limbs with phalangeal formulae of 2.3.3.2 and 2.3.3.3.2, respectively. A dermal squamation was present, but details are poorly known.

As this summary of its anatomy shows, *Trimerorhachis* was far advanced in the degenerative processes which are exhibited at a much later date in the Triassic stereospondyls. As will be noted later, certain of the degenerate features of *Trimerorhachis* are repeated in the metoposaurs, and the possibility that *Trimerorhachis* was ancestral to that group must be seriously entertained.

On the other hand, there are certain primitive features found in this genus which show that it must have diverged at a very early stage from the line leading to the typical rhachitomes. These include the retention of an essentially single condyle, of a seemingly movable basal articulation, and of an intertemporal element.

That the divergence of this type took place early in time as well as at a low stage in rhachitome development is indicated by the fact that in almost all known respects of skull roof, palate and dermal shoulder girdle, *Saurerpeton* appears to be a form which may well have been a Westphalian ancestor of *Trimerorhachis*, and already well started on the specializations and degenerative features shown in the Permian form. While many of the features observed here are quite surely degenerate rather than primitive, it is not unreasonable to assume that this developmental process took place in a form which had never progressed far toward a terrestrial type of existence.

Dawsonia

The name *D. polydens* was given by Fritsch to a number of fragmentary specimens from the very late Carboniferous "Gaskohle" of Kounová, Bohemia (1901, vol. 1, pp. 90–92, figs. 42, 43, pls. 11, 12); I have recently (Romer 1945, pp. 427–429) reviewed this material. It may represent a rhachitome of the *Saurerpeton-Trimerorhachis* type, but the identification is none too certain.

Dvinosaurus

(Figs. 3, 10, 12, 13, 22)

It is with considerable hesitancy that I discuss at this point *Dvinosaurus*, of the late Permian of the North Dvina River of northern Russia. This form occurs far later in time than other genera considered in this section, and is obviously far advanced and degenerate in many features. Nevertheless, it shows many similarities to *Trimerorhachis* and *Saurerpeton* and may represent a continuation of the same evolutionary line.

The material representing this genus was collected by Amalitsky, and described in various papers by that author (Amalitsky 1924), Efremov (1932), Sushkin (1936) and, most recently, by Bystrow (1938). Three species have been described, but it is doubtful if there is more than a single species, *D. primus*.

As pointed out by earlier writers and as confirmed by Bystrow, *Dvinosaurus* was certainly neotenous; a powerful gill apparatus is attested to by the presence of a highly developed ossified system of branchial arch elements. It is therefore possible that certain of the apparently primitive features seen in this form are to be regarded not as a direct inheritance from Carboniferous ancestors, but as the retention of larval characters which had not been present to the same degree in the adults of intervening forms.

The skull roof structure resembles that of *Trimerorhachis* and *Saurerpeton* in various respects: short face, long lacrimal, short jaws, tiny tabular, high development of lateral line grooves, and reduction of otic notch. In two conspicuous features there is marked departure from the pattern set up in that group of rhachitomes: the post-orbital region is not greatly elongated (although relatively long), and there is no separate intertemporal element. However, it might be argued that post-orbital elongation in the older genera was developed ontogenetically from a larva with a short skull. An increase in neotenic conditions might result in "fixation" of the skull shape at an ontogenetic stage prior to any great elongation of the post-orbital region. As regards the intertemporal, Bystrow (pp. 234–236) points out that the sculpture of the so-called postorbital of *Dvinosaurus* indicates that that element is actually a compound, its postero-medial portion being a fused intertemporal. We believe that Bystrow's explanation is correct. If the "postorbital" be accepted as a single element, there exists here that most unusual situation — a postorbital-parietal contact, and a separation of postfrontal and supratemporal. This

situation is found in almost no other known labyrinthodonts except the ichthyostegals — a group with which we have no reason to believe that *Dvinosaurus* had the slightest relationship.

In the palate *Dvinosaurus* likewise shows, except for its relative abbreviation, notable similarities to *Trimerorhachis* and *Saurerpeton*. As in them, the interpterygoid vacuities are of considerable size, but the pterygoid bones extend well forward on their margins. The cultriform process of the parasphenoid is flattened, the body of the bone moderately expanded; however the carotids (as in *Saurerpeton* but in contrast with *Trimerorhachis*) pass forward some distance beneath the parasphenoid before entering its substance. As in those genera, but in contrast with most earlier rhachitomes, there are anterior palatine fenestrae. The lateral teeth are (again) small and very numerous. The palatal teeth show a series pattern rather comparable to that of the genera mentioned and to advanced rhachitomes and stereospondyls, but in contrast with that of most early rhachitomes. There are, however, differences in detail. The vomerine fang-pairs are in series with the small teeth on that bone, rather than more laterally placed; the palatine is small and only a fang-pair present on it; the most anterior ectopterygoid tooth is persistently large. Seemingly highly significant is the retention of a movable basal articulation. As in *Trimerorhachis*, there is no indication of an ossified epipterygoid. Braincase ossification is further reduced than in that genus, for there has been found no trace of a sphenethmoid or either otic element; Sushkin believed a small transverse elevation on the upper surface of the parasphenoid to be the last remnant of the basisphenoid, but Bystrow points out that there is no evidence that this is not a part of the parasphenoid itself. The ridge marking in *Trimerorhachis* the posterior boundary of the basipterygoid process is here absent from the upper surface of the parasphenoid.

On the other hand, the entire occipital series is said to be present. The supraoccipital is described as small at best and present only in old individuals; otherwise a cartilage-filled gap was present between the two exoccipitals. The latter are stout but short bones, forming most of the boundary of the foramen magnum and ending dorsally beneath descending flanges of the postparietals. The exoccipitals extend anteriorly to surround the vagus foramen and include posteriorly foramina which may have been for the hypoglossal nerve — a conclusion which is, however, disputed by Bystrow. The condyle has advanced essentially to the stage seen in the typical early Permian rhachitomes, for the basioccipital is small and takes little part in the

condyle; the exoccipitals now carry most of the bony articular area.

The lower jaw is quite similar to that of *Trimerorhachis*, except that it is not as deep in the angular region; the most anterior coronoid, as well as the more posterior ones, is tooth-bearing; an anterior accessory meckelian foramen seen in *Trimerorhachis* is absent here; and the retroarticular process is more pronounced.

The vertebral column and ribs are of rather typical rhachitomous structure. Bystrow notes that in old individuals the intercentrum and pleurocentra may unite with one another and with the neural arch. The body of the animal was apparently long, with at least 36 presacrals.

The primary pectoral girdle includes but a feebly ossified scapular element. The cleithrum is present as a typical rhachitomous element capping the cartilaginous continuation of the scapula. The clavicles and interclavicle differ markedly from those of *Trimerorhachis*; they are less expanded ventrally and the interclavicle has developed a stem analagous to that of seymouriamorphans, reptiles and certain lepospondyls. The pelvic girdle is similar to that of *Trimerorhachis*. The limbs are, as in that genus, small. Humerus and femur appear to be quite similar to those of *Trimerorhachis* in such features as shaft development, small deltopectoral crest and small supinator process in the former element, heavy rounded internal trochanter, lack of outer limb of trochanteric system, and reduced linea aspera in the latter. Little can be determined regarding the feet except that the manus was four-toed.

As repeatedly noted in the description above, *Dvinosaurus* shows a structure which in almost every feature is highly comparable to that of *Trimerorhachis* and *Saurerpeton*; the only noteworthy differences, apart from greater development of neotenic features, are the shorter post-orbital skull length, the apparent fusion of intertemporal with postorbital, and the different construction of the dermal shoulder girdle. It is reasonable to conclude that *Dvinosaurus* is a descendent of the specialized group of which these genera are earlier representatives.

An alternative hypothesis is that *Dvinosaurus* has evolved from a more advanced rhachitomous form, and that the resemblances to early rhachitomes are due merely to the reappearance in the mature animal of primitive conditions retained in the larvae of advanced rhachitomes but lost in the adult ancestors. Against this, however, it may be pointed out that the structure of the temporal region practically precludes this possibility. All the more advanced rhachi-

tomes have eliminated the intertemporal, and have the postfrontal and supratemporal broadly joined. The pattern of *Dvinosaurus* here is such that it can be derived only from that of a primitive member of the Rhachitomi in which the intertemporal was present.

Previous writers have advocated the theory that *Dvinosaurus* was related to the ancestry of the brachyopids. Like *Dvinosaurus*, these Triassic forms are short-faced, and presumably resembled that genus in various other habitus characters. Like *Dvinosaurus*, the brachyopids were presumably neotenic in tendencies. But it is more than probable that this paedogenetic trend occurred at various times among the labyrinthodonts, and the similarities between the two types in such characters as the short face are features to be expected in any neotenous form. The construction of the temporal region discussed above seems to me a bar to the consideration of *Dvinosaurus* as a brachyopid ancestor, for the latter groups show in this region the construction found in more advanced rhachitomes (cf. Bystrow, 1938, pp. 271–272).

Chalcosaurus

C. rossicus was described by Meyer in 1866 (pp. 124–126, pl. 21, fig. 1) on the basis of a rather poor skull roof from the copper-bearing sandstone of the Karlaga region of Russia, presumably in Zones I or II of the current Russian classification of Permian continental deposits. The specimen, since lost, has been recently discussed by Efremov (1937, pp. 26–27) on the basis of Meyer's figures. The skull is that of a short-faced animal which, as Efremov notes, is not unlike *Dvinosaurus* in such features as can be determined. However, it is considerably longer post-orbitally than *Dvinosaurus* and, in fact, in every way approaches *Trimerorhachis* in the known structure of the skull roof. The horizon of *Chalcosaurus* is intermediate between those of *Trimerorhachis* and *Dvinosaurus*, and this form may be an actual connecting link between the two.

DISCUSSION

The "classic" examples of the Rhachitomi are the various early Permian genera, which exhibit a structural grade characteristic of the period. No intertemporal is present; the palate is firmly fused to the flattened braincase floor; the occipital condyle is essentially a

double structure, with the basioccipital practically eliminated from its articular surface. It was assumed that the rhachitomes appeared only at about the beginning of the Permian, and that for more primitive structural conditions one must turn to the Embolomeri, which were supposed to be, almost exclusively, the labyrinthodont inhabitants of the Carboniferous coal swamps.

Consideration of the genera discussed above demonstrates that this picture must be radically altered. Forms, such as *Edops,* which are unquestionably rhachitomes and appear to be proper ancestors for the characteristic Permian forms, nevertheless show structural features once believed the exclusive "property" of the embolomeres. In *Edops,* at least, the braincase shows little of the platybasic trend common in amphibians. The intertemporal bone is universally present in the forms considered in this section; the basal articulation is movable in all cases. In *Edops* and other forms the condyle is a typically primitive single structure. In some of the forms discussed the interpterygoid vacuities are widely open, but in *Edops* they are quite small and show a half-way stage between the presumably primitive closed palate and the typical rhachitomous condition.

We thus have in true rhachitomes of the *Edops* group structural features which are in many points those once regarded as diagnostic of the embolomeres. We need not, therefore, regard the embolomeres as necessarily ancestral to the rhachitomes; and, indeed, certain key points of cranial anatomy, such as the temporal and vomerine regions, strongly suggest that they were not ancestral, and that embolomerous and rhachitomous lines were distinct far back toward the still hypothetical common ancestor of the amphibians. It was pointed out in the last section that, except for orbital peculiarities of the known genera, the loxommoid group offers a primitive and reasonable point of departure for rhachitomous evolution.

Nor are the Rhachitomi confined chronologically to the Permian. *Edops,* currently the best known of primitive rhachitomes, occurs in Permian sediments but *Leptophractus* and *Gaudrya,* less well known but equally primitive, are definitely Pennsylvanian in age. It is obvious that rhachitome evolution had begun well back in the Pennsylvanian. There are as yet no known Mississippian forms (apart from the loxommids) which can be assigned to the Rhachitomi. But the appearance in the Westphalian (as noted in the next section) of more progressive rhachitomes than those here discussed suggests that the evolution of the *Edops*-like rhachitomes must have occurred by about the beginning of the Pennsylvanian, if not earlier.

Considerable variation has been noted among the genera here grouped as primitive rhachitomes. *Edops, Leptophractus* and *Gaudrya* appear to be truly primitive; *Cochleosaurus* and the *Dendrerpeton* group appear to be more advanced in the development of their interpterygoid vacuities. *Eugyrinus* and *Pelion* are very short-faced; this may be either a specialization, a neotenic feature or an indication of individual immaturity. In *Saurerpeton, Trimerorhachis Chalcosaurus* and the possibly related *Dvinosaurus* we find examples of the parallelism which is a prominent but confusing feature of labyrinthodont evolution. In this group we see the evolution, in the late Carboniferous and early Permian, of a whole series of features characteristic, not of the forms of the times, but of the Triassic labyrinthodonts. It is possible that the *Trimerorhachis* group gave rise to certain of these later types; certainly not, however, to all of them, and many common features must definitely be attributed to parallelism.

As a whole, the forms discussed in this section may be considered as a very primitive group of rhachitomes, typically Pennsylvanian in age and bridging the evolutionary and morphological gap between the presumed generalized loxommids of the early Carboniferous and the *Eryops*-like forms which appear in the late Pennsylvanian and were dominant in the early Permian. The more generalized forms — as *Edops, Gaudrya, Leptophractus,* and *Dendrerpeton* — may be considered as forming a Superfamily Edopsoidea, presumably ancestral to all later temnospondyls. The short-faced forms are more difficult to dispose of taxonomically. Some may be merely larval in nature. Others, as *Saurerpeton, Trimerorhachis* and *Dvinosaurus,* appear to be a specialized side-branch from the edopsoid level, and are best considered, perhaps, as constituting a Superfamily Trimerorhachoidea.

TYPICAL RHACHITOMES

In such typical rhachitomes as *Eryops,* characteristic of the early Permian, we find marked advances over the edopsoids, including the absence of the intertemporal bone, development of a fixed basal articulation and subdivision of the occipital condyle. Certain forms, however, while losing the intertemporal, are persistently primitive as regards other characteristics. We may in consequence regard the typical rhachitomes as constituting two successive superfamilies, the Micropholoidea and Eryopsoidea. Below are discussed micropholoids including: *Potamochoston, Lysipterygium, Micropholis, Chenoprosopus, Mytaras, Archegosaurus, Platyops* and *Melosaurus,* and

eryopsoids including: *Eryops, Onchiodon, Actinodon, Sclerocephalus, Chelydosaurus, Osteophorus,* the "branchiosaurs", *Cacops, Alegeinosaurus, Dissorophus, Broiliellus, Tersomius, Aspidosaurus, Zygosaurus, Platyrhinops, Arkanserpeton, Trematops, Acheloma, Parioxys, Mordex, Acanthostoma, Zatrachys, Platyhystrix, Dasyceps* and *Stegops.*

Departing from proper phyletic order, we will discuss *Eryops* and its close relatives before taking up the more primitive micropholoids.

Eryops

(Figs. 2, 5, 8, 10, 12, 13, 23, 25)

Although neither the oldest nor, in some regards, the most primitive of typical rhachitomes, this amphibian merits initial consideration as the type genus of the Rhachitomi and a very characteristic form. *Eryops* is a common animal in the Wichita and Clear Fork groups of the Lower Permian of Texas and adjacent states; its remains constitute perhaps half of all amphibian materials collected there. It is also represented in the geologically equivalent Abo Formation of New Mexico and in the Lower Permian and perhaps the uppermost Pennsylvanian of western Pennsylvania. A number of species have been described, apart from the genotype, *E. megacephalus.* It is probable that several species existed, characteristic of various horizons and areas, but at present there are no real grounds for specific determination. The New Mexican form has been named *Eryopsoides,* but there is no adequate basis for generic separation. The jaw fragments from the Texas Clear Fork named *Anisodexis imbricarius* probably belong to *Eryops.* Despite the large amount of known material, early descriptions of this important type were most inadequate although Case (1911, pp. 23–31, 91–104, pls. 4–10) brought together much valuable data, and Broom, Watson, and others made contributions to the study of cranial structures. Sawin, however, has published (1941) a comprehensive study of the cranial anatomy, and the writer has in preparation a description of the postcranial skeleton.

Eryops was a large amphibian, with skull lengths running to half a meter or more. In accord with the general trend of labyrinthodont evolution, the skull is rather flattened. As seen from above, its shape, with a broad rounded muzzle and the orbits rather back of the center of the length, is that which, as Watson has pointed out, is characteristic of central types in all major lines of labyrinthodont evolution. Among generic and minor features may be noted the fact

that the septomaxilla, although well developed, has lost its sculpture and hence is no longer superficial in position; the lacrimal is definitely withdrawn from the orbital area;[1] a characteristic "extra" median element is present between frontals and nasals; the facial region is much expanded (but *cf. Edops* etc.). The jaw articulation is still well posterior to the level of the occiput and there are well developed otic notches. A distinct advance over more primitive rhachitomes is

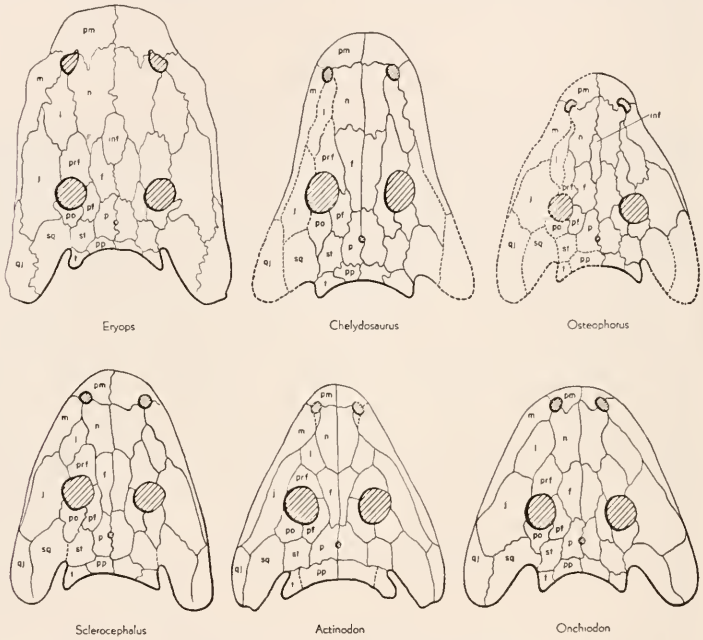

Fig. 23. Skull roofs of eryopsids. *Eryops* after Sawin; *Chelydosaurus* after Fritsch, Steen; *Osteophorus* after Meyer; *Sclerocephalus* after Branca; *Actinodon* after Gaudry, Thevenin; *Onchiodon* from data in Geinitz and Deichmüller, Credner.

the absence of the intertemporal. There is no evidence of its fusion with any adjacent element, and we may reasonably assume that here (as presumably in loxommids) the intertemporal center of ossification, never greatly developed, had gradually disappeared. Its former area is taken over by the adjacent elements, postfrontal and supra-

[1]In *Eryops* the lacrimal still reaches the narial region, but in most of the forms in this and more advanced stages of evolution, it has withdrawn from the borders of nostril as well as orbit.

temporal, which (in contrast to conditions in ichthyostegals) are broadly in contact.

In palatal view, most features of the skull are readily comparable with those seen in *Edops*. The palatal teeth include (apart from a shagreen of denticles) single fang-pairs on each of the three lateral elements, with none of the tendency toward linear arrangements already seen in *Trimerorhachis* and occurring again in more advanced types. The marginal teeth are large; *Eryops* was presumably a predaceous form. The palatal vacuities are moderately enlarged, as compared with *Edops*, but no larger than in some of the genera already discussed; the pterygoids still extend broadly forward to the vomers. The basal articulation, however, has changed significantly. Motility is completely lost. In the articular area, the basisphenoid still projects outward into a socket formed by pterygoid and epipterygoid (cf. Sawin, pl. 3, BSPH); but this once movable joint is immobilized by a stout sutural union of parasphenoid with pterygoid around its anterior, ventral and posterior surfaces. In contrast with more advanced rhachitomes, it will be noted that the area of union of palate and braincase is still a narrow, rounded bar, and confined to the region of the original articulation. There is a well developed epipterygoid.

The cultriform process of the parasphenoid is somewhat flattened; the body of the bone is not excessively expanded. The carotids do not enter the bone until they have passed forward to the pituitary region, a situation contrasting with their longer intra-parasphenoidal course in various genera of both earlier and later times. The occiput is ossified; more so than in *Edops*, for example, for both paroccipital process and supraoccipital area are complete. There are no indications of sutures between exoccipitals and the supraoccipital region, and there is no evidence that a separate supraoccipital was present. The basioccipital is present and takes part in the condyle. This structure, however, is no longer of the primitive single circular type, but rather broad and tripartite, with lateral exoccipital areas carrying much of the articular surface. In contrast to many advanced forms, the otic region is fully ossified, and a continuous braincase wall runs forward to the well ossified but rather flattened sphenethmoid. The lower jaw shows in most features a typical rhachitomous structure. The coronoids are almost toothless although there are small denticles on the posterior bone of the series; there is no retroarticular process.

Practically complete skeletons are known. The body of *Eryops* was rather high and but moderately broad, showing little of the

flattening tendency seen in the head. There were but 23 presacral vertebrae, a much smaller number than in (for example) *Trimerorhachis* or certain of the embolomeres. The vertebrae are typically rhachitomous, with well ossified inter- and pleurocentra and tall neural spines (a feature presumably associated, in part at least, with the large size of the animal). There was a characteristic labyrinthodont ventral squamation and a lateral and dorsal covering of feebly ossified scales presumably buried in the skin (Romer and Witter 1941).

In the dermal shoulder girdle, the cleithrum was of the capping type. Clavicles and interclavicle were little expanded ventrally and but feebly sculptured; presumably they had sunk deep within the dermis. The scapulocoracoid was fully ossified and developed from a single center. The pelvis also was completely ossified, including a massive pubis; the ilium was a vertical blade, with but a slight spur to represent the posterior expansion seen in various Carboniferous amphibians.

The limbs (cf. Romer 1922; Miner 1925) were rather short, but very massively developed — *Eryops* was as well adapted for terrestrial life as many of his reptilian contemporaries (we may note, in this connection, the absence of lateral line grooves on the skull of *Eryops* and a majority of typical rhachitomes). The humerus is of the typical tetrahedral type, with no shaft region and with very pronounced processes at either end. The femur has all segments of the ventral ridge system well developed, and a characteristic detail is the V-shaped ridge surrounding the distal dorsal intercondylar fossa. The manus is known from two specimens (one described by Gregory, Miner and Noble 1923), and was of a four-toed primitive type; specimens of the pes, as yet undescribed, show a structure similar to that of *Trematops*.

We cannot readily compare the postcranial skeleton of *Eryops* with that of older or more primitive rhachitomes because of the inadequate nature of the material of these forms. As regards the cranial structure, however, *Eryops* might find in almost all respects a reasonable ancestor in members of the *Edops* group.

Onchiodon

(Fig. 23)

Eryops was, as far as known, confined to North America. In Europe, however, there are contemporary forms which were intimately related.

As pointed out by Watson (1919, pp. 4–5), the closest relative appears to be *Onchiodon labyrinthicus*, the only large amphibian from the famous Lower Permian deposits of Niederhässlich (Plauen'scher Grund) near Dresden. Credner (1893, etc.) gave descriptions of a number of imperfect skulls and of a fair amount of postcranial material.

In addition to material generally ascribed to *O. labyrinthicus*, specimens from Niederhässlich which are probably *Onchiodon* have been described under various other names. The writer has noted (1925) that part of the material described as a cotylosaur, *Stephanospondylus*, really belongs to the present genus, but that on the other hand a foot assigned to this form by Credner and Jaekel is that of a pelycosaur (Romer and Price 1940, p. 306). As discussed elsewhere, the "branchiosaur" material from Niederhässlich (*"Branchiosaurus"*, *"Pelosaurus"*) appears to consist of young *Onchiodon* individuals, and in various regards (particularly the dermal shoulder girdle) shows eryopsid features. *"Archegosaurus" latifrons* of Geinitz and Deichmüller (1882, pp. 21–23, pl. 6) seems to be a partly grown *Onchiodon*, as is the supposed *Archegosaurus latirostris* of this locality (Credner 1882, pp. 235–237, pl. 13, figs. 6–8), assigned to *Melanerpeton* by the former writers (1882, pp. 23–27, pl. 8). Still further, a Niederhässlich specimen which Credner (1882, pl. 13, figs. 9–14) thought to belong to *Archegosaurus decheni* (of the Saar Permian) shows nothing characteristic of that long-snouted animal and agrees well with *Onchiodon*.

This Niederhässlich rhachitome has frequently been assigned to *Sclerocephalus*, discussed below; but as Watson points out, the two are readily distinguishable in the construction of the dermal shoulder girdle and other features.

I have recently (1939a, fig. 2) restored the dorsal surface of the skull on the basis of the data given by Credner and by Geinitz and Deichmüller. Few of the individuals represented are of large size, the largest skulls known being on the order of 12 to 15 cm. in length; this, Watson reasonably suggests, is related to the fact that the Niederhässlich deposits contain primarily the remains of water dwellers, whereas the truly adult *Onchiodon* would have been, like *Eryops*, a more or less terrestrial form.

The skull roof pattern is very similar to that of *Eryops* except that the interfrontal of the latter genus is absent and the face is much less expanded — a feature which appears to be associated with smaller absolute size. Such palatal and jaw material as is known is also *Eryops*-like. The postcranial skeleton is represented by vertebrae, ribs and various girdle and limb elements, all of which are practically

identical with the homologous *Eryops* structures, and the two genera appear to be very closely related.

At Kounová, Bohemia, the Gaskohle deposit, situated stratigraphically almost on the Carboniferous-Permian boundary, includes numerous fragmentary remains of rhachitomes described by Fritsch (1901) under a variety of names—*"Dendrerpeton" foveolatum, "Macromerion" abbreviatum, "M." bicolor, "M". ? pauperum, "Branchiosaurus" robustus, "B." venosus, "Limnerpeton" dubium, Porierpeton nitens.* I have recently (1945, pp. 425–427) discussed this material. Some of it, at least, pertains to a typical rhachitome allied to *Onchiodon* and *Eryops,* and I have grouped it under the name of *Onchiodon? foveolatum.*

Actinodon

(Fig. 13, 23)

A. frossardi appears to have been the common large labyrinthodont of the early Permian of the Autun coal basin of France. Much of the material was described in various papers by Gaudry (1883, 1887, 1888, etc.) and Thevenin (1910) (cf. Watson 1919, p. 6). The type material was that of a small animal; large specimens, of the size of *Eryops* but apparently cospecific, were once believed to belong to a separate genus and species, *Euchirosaurus rochei*; *Actinodon brevis* is still another synonym. The "branchiosaurs" *Protriton petrolei* and *Pleuronoura pellati,* and material assigned to *Pelosaurus laticeps,* all from the same locality, appear to be larval specimens of the same amphibian; *Protriton fayoli,* from a slightly earlier horizon (late Stephanian) of the same basin, may also be a larval *Actinodon. "Archegosaurus" latirostris* of the Lebach beds of the Saar basin (Meyer 1857, pls. 9, 10, etc.) is usually regarded as generically identical with the Autun form and is at any rate closely allied.

The skull is of the generalized rhachitomous type; it differs little from *Onchiodon, Eryops* or *Sclerocephalus* in most respects. However, the face is much less expanded than in *Eryops,* and in *A. latirostris* it is relatively slender. The tabular region is more rounded and expanded than is normally the case, and an interesting variant in pattern is that the lacrimal extends postero-medially to meet the frontal. This last feature is seen in the *"Protriton"* larva as restored by Bulman and Whittard (1926, fig. 7), although not in the restoration of Thevenin (1910, fig. 5), and in certain Autun specimens assigned to *"Branchiosaurus"* (cf. Fig. 24). The posterior part of the palate is known, and

is comparable to that of *Eryops* except that the interpterygoid vacuities are somewhat larger. The occipital condyle is similar in structure to that of *Eryops*. Considerable postcranial material is described from Autun. In almost every respect this is strikingly similar to material of *Eryops* or *Onchiodon*. However, as Watson has pointed out, the clavicles and interclavicle are more expanded and more prominently sculptured than is the case with *Eryops*, and certain of the vertebrae figured by Gaudry show, in contrast to *Eryops*, a marked lateral expansion at the top of the neural spine somewhat analogous to the aspidosaur condition. The genus is certainly distinct from *Eryops* and *Onchiodon* but equally certainly closely related. Watson would separate this form (and *Sclerocephalus*) from the former genera at the family level because of the differences in the dermal girdle, but it seems to the writer preferable to emphasize the marked similarities rather than relatively minor differences, and to include all these forms in a single family.

Sclerocephalus

(Figs. 23, 25)

Essentially contemporaneous with *Onchiodon* and *Actinodon* is *Sclerocephalus häuseri* of the Lower Permian of the Rheinpfalz. Besides the type, described by Goldfuss (1847) and Meyer (1857, pl. 15), the remains include several other specimens reasonably ascribed to the species by Ammon (1889) and Broili (1926); the material affords much data concerning the skull and anterior part of the body. In addition, it was early recognized that an excellent skull described by Branca (1886) as *Weissia bavarica* pertained to *Sclerocephalus*, but since it is from a somewhat lower (Cuseler) stratigraphic level than the type, it may be specifically distinct. Material from Niederhässlich, Bohemia and Silesia has been assigned to this genus, but apparently incorrectly. "*Macromerion*" *guembeli* of Ammon (1889) is known only from a fragment of the jaw margins of a large labyrinthodont from the Lower Permian of the Rheinpfalz. It is possible that this represents a large individual of *Sclerocephalus*, the common amphibian of that horizon and region.

The skull material shows a normal rhachitome, comparable in almost all respects to the genera discussed earlier in this section, but lacking the expansion of the face seen in *Eryops* and the peculiar lacrimal relations of *Actinodon*. The palate is fairly comparable to

that of *Eryops*, but with slightly larger interpterygoid vacuities and with an additional tusk-pair on the palatine or ectopterygoid. As Watson notes (1919, p. 4), the clavicles and interclavicle are sculptured and expanded ventrally, and thus more like those of *Actinodon* or *Chelydosaurus* than those of *Eryops*.

There is a variety of material from the Palatinate which may represent the young of *Sclerocephalus*. This includes a small skull found on the same slab with Ammon's mature specimen and referred by him to *Branchiosaurus amblystomus*, and a skull table and partial axial skeleton of a small individual from the same beds named by him *B. caducus*. Further material from the Palatinate which may belong here is noted in the discussion of the "branchiosaurs".

Chelydosaurus

(Fig. 23)

C. vranii was described by Fritsch in 1885 (1901, vol. 2, pp. 18–27, pl. 56) on the basis of three skulls and various posteranial fragments from the Lower Permian of Broumov, Bohemia; to this material he later added a nearly complete skeleton from the same locality (vol. 4, fig. 393). Fritsch's material and still further specimens in the Prague Museum have been more recently studied by Steen (1938, pp. 248–249, fig. 34). *"Actinodon" germanicus*, recently described from Broumov (Braunau) by Kuhn (1939), differs in no known feature from *C. vranii*. Kuhn cites as a difference the fact that the tabulars are pointed in *Chelydosaurus*, but not in his specimen. But, to judge from his photograph of the material, the evidence is not convincing.

The skull roof shows the typical pattern of contemporary rhachitomes, but with rather greater elongation than usual, particularly in the facial region. Steen believes the various specimens ascribed to *Chelydosaurus* to be cospecific, but, as she notes, there appears to be considerable variety in skull shape in the material. For example, our illustration is made from a specimen (Prague Museum, No. 350) which Steen selected as the lectotype; No. 345, figured by Fritsch (pl. 57, fig. 1) is much shorter in the post-orbital region. The body, in correlation with skull proportions, appears to have been relatively long and slender; the vertebral count appears to have been a normal number of about 24 presacrals, but the individual vertebrae are somewhat elongated. The interclaviele, too, is a rather elongate rhomboid. Limbs were moderately developed, a good ventral squam-

ation present. A partial foot appears to give a count for the last three digits of 4.4.3. *Chelydosaurus* appears to have been an elongate variant of the typical eryopsid pattern.

Osteophorus

(Fig. 23)

A poorly known European amphibian which may be related to *Eryops* is *O. roemeri,* described by Meyer (1860) on the sole basis of the impression of a skull roof from the Lower Permian (Lebach stage) of Klein-Neundorf in the North Suedetic basin of Silesia. As Watson has noted (1919, pp. 5–6), this form is strikingly similar to *Eryops* in the development of an interfrontal element, but differs in other features, such as the narrower muzzle, apparent entrance of the frontal into the orbital margin, shorter lacrimal, and rather slit-like nostrils. In default of data on the palate, one cannot be sure of the relationships of *Osteophorus,* nor discount the suggestion of relationship to *Melosaurus* given by the constriction of the muzzle.

"Branchiosaurs"

(Fig. 24)

It may be appropriate to discuss at this point the small amphibians of the Lower Permian which, as "*Branchiosaurus*" and allied genera, constitute the main stock of the supposed Order Phyllospondyli; for it appears that these creatures are for the most part larvae and young of the typical rhachitomes just discussed.

The best known members of this group are *Branchiosaurus amblystomus* and *Pelosaurus laticeps* from Niederhässlich, described by Credner and other authors on various occasions (Credner 1885, 1886, etc.; Watson 1940, pp. 225–227, figs. 22, 23). All specimens of these forms are of small size, and the smaller individuals of *B. amblystomus* were gill-bearing. It was assumed that the somewhat larger forms were adults which were supposed to differ from labyrinthodonts not only in size but in certain structural features which merited the erection, for these and similar forms, of the Order Phyllospondyli. Small animals of the same sort have been described from various European localities of early Permian and late Carboniferous age and were naturally assigned to the same group. An additional impetus toward expansion of the group came with the description

by Watson of *Eugyrinus* (discussed earlier) from a horizon well down in the Pennsylvanian. This little form was assigned to the Phyllospondyli because of obvious similarities to the typical branchiosaurs; its general evolutionary grade was that of a Permian rhachitome among the (supposedly unrelated) Labyrinthodontia. In consequence, when various Carboniferous types from Linton, Ohio, were discovered which were rhachitome-like in structural development

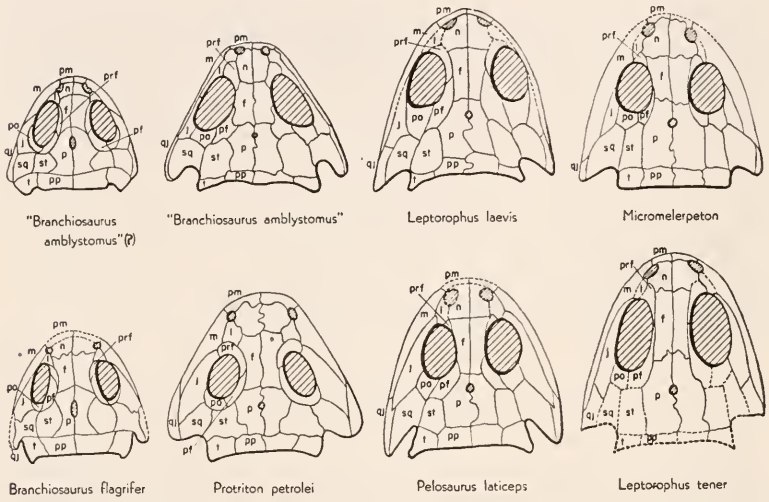

Fig. 24. Branchiosaurs. *"Branchiosaurus amblystomus"* (?) from Odernheim, after Bulman and Whittard; *B. amblystomus* from Niederhässlich after Watson; *Leptorophus laevis* after Bulman; *Micromelerpeton* after Bulman and Whittard; *B. flagrifer* after Whittard; *Protriton petrolei* after Thevenin, Bulman and Whittard; *Pelosaurus laticeps* from Odernheim after Bulman and Whittard; *Leptorophus tener* after Bulman and Whittard.

of the skull, but supposedly too early in age to be Rhachitomi (then thought to be exclusively Permian), they were assigned by both the writer (1930) and Steen (1931) to the Phyllospondyli.

This overexpanded Order "Phyllospondyli" appears, however, to have collapsed under its own weight. It now appears probable that no such group exists. The Carboniferous forms are small and sometimes immature labyrinthodonts of one sort or another; the typical Permian branchiosaurs are stages in the development of typical rhachitomes described above. The evidence has been presented in a recent paper (Romer 1939a) and need not be repeated here.

In a still more recent work by Watson (1940), which had gone to press before the appearance of my discussion of the subject, he retains the Order Phyllospondyli in a modified form, including four families of small Carboniferous and Permian amphibians. The definitive features are here said to lie in the vertebral construction (pp. 228–229), in which the neural arch is thought to extend downward around the notochord and to cover much of the area normally occupied by the central elements. But this situation is known only in the *Miobatrachus* group of presumed frog ancestors, which show no affinity of any sort to the more typical branchiosaurs; in the other three families the neural arches, as far as I am aware, do not seem to be unduly extended ventrally. Of these three families, the Eugyrinidae are characterized by features found in primitive rhachitomes of the group to which I believe *Eugyrinus* to belong; the Melanerpetontidae are characterized by the presence of features of the Seymouriamorpha, in which group I believe *Melanerpeton* should be placed. The characteristics of the supposed Family Branchiosauridae (Watson 1940, p. 229) are essentially those defining a typical rhachitome, or, rather, an immature individual of that group.

Only one positive diagnostic feature appears to separate a "branchiosaur" from a rhachitome. This is the statement that in the branchiosaurs the ectopterygoid is absent, whereas this primitive element is present in the normal rhachitome palate. This apparent absence of the ectopterygoid appears, however, to be due to the nature of the immature skull material. A parallel is found in the case of *Archegosaurus*. In the more mature specimens of this rhachitome (Fig. 28) the ectopterygoid is, of course, present; in the larval form, Whittard (1928, p. 259, fig. 1) notes that this element — small, weak, perhaps slow to ossify, and at first loosely attached to its neighbors — is seldom found and was in fact not present in the material available to him.[1] It would be absurd to classify the young *Archegosaurus* as a member of the "Phyllospondyli" because of its lack of an ectopterygoid, and there is, by the same reasoning, no justification for believing the "branchiosaurs" to be members of such a group. There is currently no basis for definition of an "Order Phyllospondyli", and equally little basis for believing the "branchiosaurs" to be other than larvae of typical rhachitomes.

Of the Permian branchiosaurs, it seems certain that the Niederhässlich forms — *B. gracilis, amblystomus, Pelosaurus laticeps* — are

[1]The history of the lacrimal is comparable. Its absence was once thought to be a diagnostic character of "branchiosaurs"; but it is now known to be present in such forms.

varied growth stages of the typical rhachitome of that locality, *Onchiodon*.[1] At Autun is found a similar series of small forms — *Protriton petrolei, P. fayoli, Pleuronoura pellati, "Pelosaurus"* — which seems equally certain to represent the young of *Actinodon frossardi*.

There are, however, various other European Lower Permian "branchiosaurs" which exhibit similar characters and hence are presumably young rhachitomes, but which cannot be as definitely correlated with mature animals. It is possible that much of this material may belong to *Chelydosaurus* or *Sclerocephalus*.

In the Broumov region have been found numerous "branchiosaurs", of which the greater part are probably young of *Chelydosaurus*. *Melanerpeton pusillum* (Fritsch 1901, vol. 1, pp. 96–99, figs. 48–50, pl. 13; Steen 1938, p. 256; figs. 38a, 39a; Augusta 1938, 1939), a small gill-bearing form, differs markedly from the other species assigned to that genus, and appears in all probability to be a young rhachitome tending toward the skull elongation seen in the adult *Chelydosaurus*.[2] *"Branchiosaurus" umbrosus* from the same locality (Fritsch 1901, vol. 1, pp. 81–82, pl. 6) is a still more immature type of larva which Augusta has reasonably interpreted as identical with the last. It will be noted that *pusillum* is the genotype of *Melanerpeton* and that name should replace *Chelydosaurus*, a more recent name, if identity of larval with adult material should be firmly established.

Possibly belonging to *Sclerocephalus* are numerous "branchiosaurs" of Lebach age from Saxony and the Rheinpfalz; much of this material has been described in various papers by Bulman and Whittard (1926), Bulman (1928), and Whittard (1930). We have earlier noted two "branchiosaurs" from the Palatinate found in the same beds with *Sclerocephalus* which are probably the young of that form. In addition, there have been described from Odernheim in the Palatinate *Leptorophus laevis, Micromelerpeton credneri*, and forms identified as *B. amblystomus* and *Pelosaurus laticeps*; from Jacobsweiler, also in the Palatinate, *Pelosaurus guembeli*; from Friedrichroda in Thuringia, *"Branchiosaurus" flagrifer* and *Leptorophus tener*. All these are typical "branchiosaurs" and hence larval specimens of typical rhachitomes. The material assigned to *"Branchiosaurus"* from these localities consists of short-faced individuals. It will be noted that in contrast to the Niederhässlich material of *"Branchiosaurus,"* there is a good contact of frontal with lacrimal, a feature definitely known among

[1]Whether the material described under these names at other localities is cospecific is doubtful.

[2]Augusta's contention that *M. pusillum* may be the young of *M. pulcherrimum* has little foundation; the basic skull pattern (not merely the shape) is entirely different. Cf. *Phaiherpeton*.

adults only in *Actinodon* and in the obscure rhachitomes *Potamochoston* and *Lysipterygium*, described below. The *Leptorophus*, *Micromelerpeton* and *Pelosaurus* (?) specimens are larger and, perhaps merely in consequence of this fact, longer headed. There is little difference between these forms that cannot be attributed to accidents of preservation and individual and specific variation. If they are the young of known rhachitomes of Lebach age, *Archegosaurus*, *Osteophorus* and *Actinodon* are out of the question because of technical features of skull roof construction; association with *Sclerocephalus* is reasonable, but proof is lacking.

Potamochoston

(Fig. 26)

We have noted four key characters which distinguish the typical rhachitomes from primitive forms: these have to do with (1) large size of interpterygoid vacuities; (2) loss of intertemporal element; (3) division of occipital condyle; (4) fusion of palate and braincase at the basilar articulation. Some forms which are quite primitive in other features had already undergone considerable enlargement of the vacuities; loss of the intertemporal appears to have occurred rapidly and generally in most rhachitomous lines. Condylar subdivision appears to have gone on, however, at a slower pace, and modification of the basal articulation seems to have been a relatively late occurrence. Beginning with the present genus, we shall discuss a variety of forms which were progressive in other ways but tended to retain a single condyle and were persistently primitive in the retention of a movable articulation between palate and braincase. We must, however, point out that interpretation of the condition of the basal articulation is highly susceptible to error, since parasphenoid and pterygoid, even if immovably joined in life, tend to separate in fossil material if the underlying endochondral elements are not well ossified — a situation frequently encountered in small or immature animals.

We may begin consideration of this transitional class of rhachitomes here considered as constituting a Superfamily Micropholoidea, with "*Limnerpeton*" *latieeps*, known from a single specimen (Fritsch 1901, vol. 1, pp. 141–151, pl. 31; Steen 1938, p. 261) from the early Stephanian of Nýřany (a supposed second specimen from Třemošná is, as Steen notes, a lepospondyl). This is a slab containing most of the skull roof and part of the postcranial skeleton of a small rhachitome,

showing in almost every respect diagnostic features of the typical early Permian rhachitomes and their larval representatives. The skull, about 33 mm. long, is short-faced, perhaps due to immaturity. There is no intertemporal, but presumably a well developed supratemporal. As figured by Fritsch, the frontal and lacrimal appear to be in contact — an unusual condition, but one which we have seen in *Actinodon* and apparently present in certain "branchiosaur" larvae. The vertebrae, ribs, girdle and limb bones are, as far as can be determined, those of a typical rhachitome; the clavicles are very similar to those of *Eryops* and *Onchiodon*.

Little or nothing, unfortunately, can be said of the nature of the occipital condyle or the basal articulation in this specimen. This deficiency, however, can be remedied by a consideration of *Potamochoston limnaios*, described by Steen (1938, pp. 250–252, figs. 36–37). The material from Nýřany consists of a skull and fragmentary postcranial remains of a slightly smaller rhachitome which in almost every respect is closely comparable to and presumably identical with *Limnerpeton laticeps*. The general structure and proportions of the skull are similar, and the similarity extends even to such details as the shape of the tabular projections and the occipital lappets of the postparietals. The dorsal surface is, unfortunately, far from completely known, but much of the palate is preserved. This shows (as expected) rather large interpterygoid vacuities. But there are two primitive features. The basal articulation is a freely movable one, and Steen's illustrations show that the occipital condyle was still a single structure. We thus have in *Potamochoston* a form transitional between primitive and typical rhachitomes.

Branchiosaurus salamandroides of Nýřany was the first described branchiosaur. It is represented by numerous specimens (Fritsch 1901, vol. 1, pp. 69–81, pls. 1–5; Bulman and Whittard 1926, pp. 549–553, figs. 5, 6). As the latter writers point out, it is by no means certain that all of this material is cospecific. It is certain, however, that most of it is of a larval rhachitome type, and various specimens show features suggestive of *L. laticeps* and *Potamochoston* in, for example, the elongate postfrontals, anterior expansion of the frontals, *Eryops*-like dermal girdle, etc. Bulman and Whittard (1926, pp. 552–553) note a four-toed manus and five-toed pes with formulae of 2.2.3.2 and 2.2.3.4.3. All in all, it seems reasonable to assume that *Branchiosaurus salamandroides* is the larval form of *Potamochoston*. Stehlik (1924, pp. 271–272, figs. 3, 4) has described specimens from Nýřany as *B. gracilis*, which presumably belong here as well.

It is possible that this animal grew to greater size than the first two specimens here described. *Sparagmites lacertinus* (Fritsch 1901, vol. 2, pp. 15–16, pls. 50, 52) is known from two Nýřany specimens showing rhachitomous vertebrae and limb bones. The size is somewhat greater than that of *Limnerpeton laticeps*, but there are no features indicating that the two might not be identical.

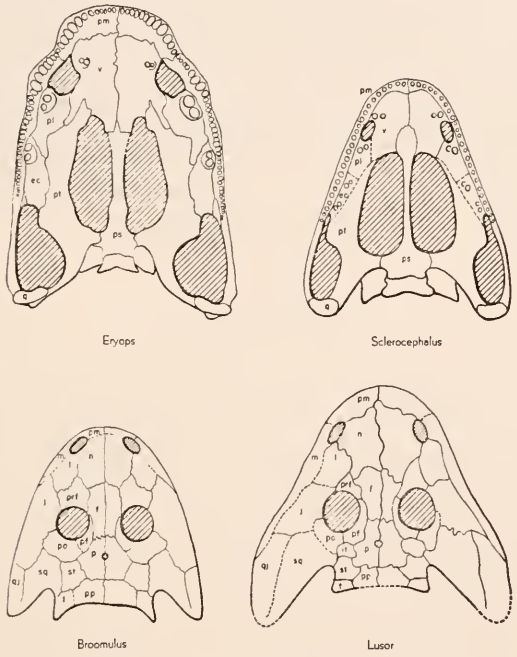

Fig. 25. Rhachitomes. *Eryops* after Sawin; *Sclerocephalus* after Broili; *Broomulus* after Broom; *Lusor* after Steen, Fritsch.

A still larger animal — one which may have approached in size some of the small individuals of *Eryops*, for example — is "*Macromerion*" *bayeri* (Fritsch 1901, vol. 2, pl. 64) .This is represented by various slabs bearing fragmentary, unassociated remains of belly scales, rhachitomous vertebrae and a partial shoulder girdle (cleithrum, coracoid and ?interclavicle), with a very eryopsid appearance.[1]

[1]This most characteristic specimen may be designated as the holotype. The remains were mistakenly identified by earlier writers as the pelvis.

This "species" may represent an adult of the *Potamochoston* type. But it must be noted that the features of *Sparagmites* and *M. bayeri* are merely those of rhachitomes in general, and these remains may well belong to one of the more primitive Nýřany rhachitomes discussed earlier.

The nomenclature of this early rhachitome presents a delicate problem. *Limnerpeton* and *Macromerion* have as genotypes animals quite different from rhachitomes of this sort; *Sparagmites* in itself shows nothing to distinguish the animal here considered from any other rhachitome. *Branchiosaurus* is the first available name and, if laws be followed strictly, should be used for this Nýřany animal. But it has been, and is, used so widely for Permian rhachitome larvae that such use would lead to confusion. Pending possible future "legal" resolution of the problem, it seems preferable to refer to the present form as *Potamochoston salamandroides*.

Lysipterygium

(Fig. 26)

This relatively primitive stage of rhachitomous evolution — one in which the interparietal is lost, but motility persists in the basal articulation — is repeated in a number of other forms from the late Carboniferous, Permian and earliest Triassic. Certain of these, discussed later, are specialized, long-snouted types. There are, however, a few forms of this sort with more normal skull shapes, of which *Lysipterygium* is one.

L. deterrai (Branson 1935, pp. 23–26, fig. 2, pl. 1, fig. 1) has as a type a slab containing much of the skull and jaws, plus a few postcranial elements; the specimen was obtained from the Lower Permian *Gangamopteris* shales near Zewan, Kashmir. Little can be seen of the skull roof, but the palate is distinctly primitive in the retention of a movable basal articulation. The specimen suggests the presence of a relatively narrow and single condyle. The pterygoids and the central area of the parasphenoid are heavily denticulated. As in a number of other Permian and Triassic temnospondyls, there is developed a longitudinal series of teeth on the palatine and ectopterygoid; the vomer, unfortunately, is incomplete and its dentition unknown. An unusual feature is the separation of the choanae from the premaxillae. The clavicles and interclavicles are moderately developed ventrally and well sculptured.

Little can be seen of the skull roof except for the interorbital region; but Branson points out that it is reasonable to believe that his form is generically, if not specifically, identical with "*Actinodon*" *risinensis* (Wadia and Swinton 1928) from the same Kashmir beds, and known from the skull roof alone. This presents the pattern of a generalized rhachitome type, in which the only marked specialization is a contact between lacrimal and frontal; this unusual condition is seen otherwise in *Actinodon* and in *Potamochoston*, giving credence to the belief that *Lysipterygium*, as suggested by its palatal structure, is related to the latter type.

No member of this group has been described from the Lower Permian of North America; however, an undescribed skull from that region appears to be of this type.

Micropholis

(Figs. 12, 13, 26)

A very late survivor of the *Potamochoston-Lysipterygium* group is apparently seen in *Micropholis stowi* [*Petrophryne granulata*] from the basal Triassic (*Procolophon* Zone) of South Africa (Huxley 1859, pp. 642–647, pl. 2; Owen 1876; Watson 1913; Broili and Schroeder 1937). This was a small rhachitome; since there are numerous specimens, all approximately of a size, the primitive features of the genus cannot be attributed to immaturity. The skull is rather short-faced, and the orbits are large, in correlation with the small size of the animal. The otic notch is very large, the jaw condyles in advance of the occipital plane. The lacrimal extends, in primitive fashion, from narial region to orbit; the frontal enters the orbital margin; the jugal is confined to the preorbital region; all are features associated with large orbital size. A median opening between the premaxillae may be related to some type of gland. Watson described in the temporal region a large element which seems homologous with the supratemporal, and a very small posterior element adjacent to the otic notch; Broili and Schroeder could not be sure of the presence of the latter element which, if present, is perhaps a neomorph. The palate is notable for the persistence of the movable basal articulation: a condition otherwise unknown after the Lower Permian except in *Dvinosaurus*. The vomers are large; the lateral portions of the palate are poorly known, but the pterygoids certainly did not extend far forward lateral to the large interpterygoid vacuities. As in the last

genus, the premaxillae do not enter the borders of the choanae. Parasphenoid and pterygoid are denticulate; the dentition of the other palatal elements is not adequately known, but none of the teeth appears to have been large. There was no ossified supraoccipital and the condyle appears to have been essentially double, borne by the two exoccipitals, with a reduced basioccipital between them. There are distinct remains of ossified branchial arches, indicative of neotenous tendencies.

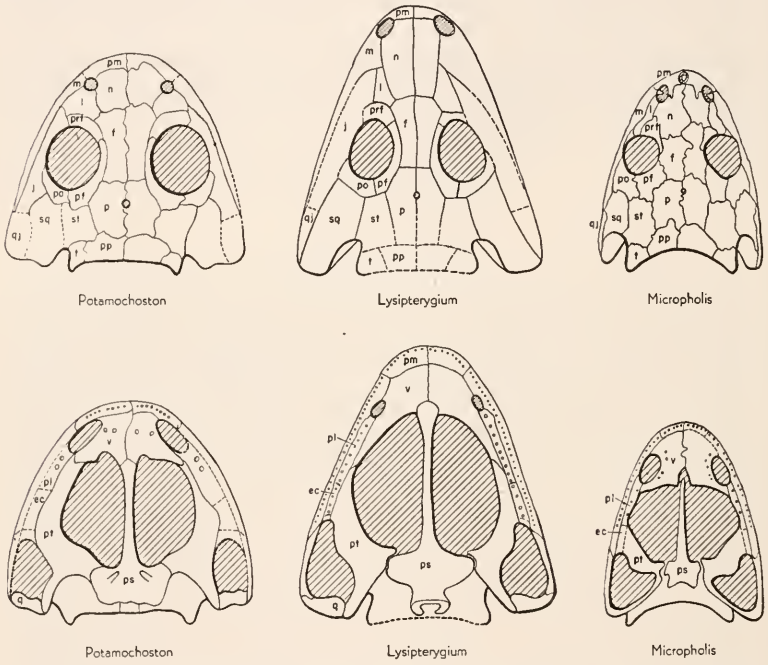

Fig. 26. Normal-skulled micropholoids. *Potamochoston* after Fritsch, Steen; *Lysipterygium* after Branson, Wadia and Swinton; *Micropholis* after Watson, Broili and Schroeder.

The vertebrae are distinctly rhachitomous, with highly developed pleurocentra. The body was short (20 presacrals). Scapulocoracoid and pelvis are (including the pubis) well ossified, indicating maturity of the material studied and a lack of degenerative tendencies in the posteranial skeleton. The dermal shoulder girdle is little expanded

ventrally. The limb skeleton is well developed, and even much of the carpal and tarsal region well ossified. The major limb elements are of good size although (as expected in a small form) not greatly expanded transversely; obviously *Micropholis* was capable of satisfactory progression on land. The feet have characteristic rhachitomous formulae of 2.?2.3.3 and 2.2.3.4.3.

Evidently *Micropholis* is a persistently primitive representative of an early stage of rhachitomous evolution. The primitive features seen cannot be accounted for by neoteny, for any suggestion of a trend in this direction which might be deduced from the ossification of visceral arches is countered by the high degree of ossification of the skeleton and the well developed limbs.

Säve-Soderbergh (1935, p. 90) states that *Micropholis* and the dissorophid *Broiliellus* are closely related and "need hardly be put into separate families." Apart from the fact that both are short-faced and have large otic notches, it is difficult to see what could have suggested such an association.

Chenoprosopus

(Fig. 27)

From the rhachitomous stage in which the basal articulation was still movable but other features were advanced in nature, there appears to have branched off a number of long-snouted forms. One such is *Chenoprosopus milleri*, known from two skulls from the Lower Permian of New Mexico (Mehl 1913; Williston 1918, pp. 93–95, fig. 7). Neither specimen is complete, and a number of points of construction, particularly with regard to the skull table and braincase, are unknown or uncertain. The skull is that of a relatively large form with a greatest length of about 30–35 cm. The general contours are rather like those of an alligator, for the snout, although persistently broad, is much elongated and greatly flattened. There are little data on the pattern of the skull table elements, but they appear to have been of the normal rhachitomous pattern. The palate is an elongate modification of the primitive rhachitomous type. There was a moderately slender parasphenoid, above which was an ossified sphenethmoid; the pterygoid was persistently movable in its basilar connection with the braincase, the more posterior part of which is unknown. The interpterygoid vacuities are not greatly enlarged, and it is probable that the pterygoids reached far forward (not, however, forward to the

narial openings as suggested by Williston). The palatal dentition appears to have been of the primitive pattern, with a tusk-pair on each lateral element. The choanae are remarkable, elongated structures. Their anterior ends are directly beneath the external nares; their posterior continuation suggests an "attempt" to construct a false palate of a sort; possibly the anterior part of the choanae may have been membrane-covered in life, and the actual opening may have been to the rear as an improvement in air breathing in a water dweller.

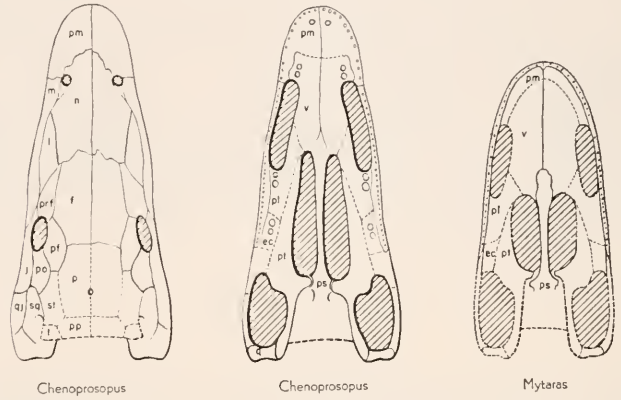

Fig. 27. Chenoprosopids. *Chenoprosopus* after Mehl, Williston and specimens; *Mytaras* after Steen.

This alligator-like form was presumably an offshoot from a rhachitome in the *Potamochoston* stage of development. It may be noted, however, that since the temporal region is poorly known, there might have been an intertemporal element indicating divergence from a still lower, *Edops*-like stage.

Some material from the lower levels of the Wichita group indicates the presence in Texas of a form related to or identical with *Chenoprosopus*. A rhachitomous vertebral column is associated.

Mytaras

(Fig. 27)

A possible Pennsylvanian ancestor of *Chenoprosopus* is *Mytaras macrognathus* from the Westphalian of Linton, Ohio (Steen 1931, pp. 868–869, fig. 14), represented only by a small and fragmentary skull

which shows little except the jaw margins and the central area of the palatal surface. Obviously the anterior part of the skull was much elongated, and the snout very broad, with great development of the vomers, all as in *Chenoprosopus*; the palatal vacuities were moderately developed, the basal articulation freely movable, as in that genus; the lateral teeth were numerous but slender, also as in *Chenoprosopus*. Steen has restored the lateral portion of the palate according to the plan of the more normal rhachitomes; I have, equally legitimately, restored this area after the fashion of *Chenoprosopus*. Few details of the skull roof are visible. Expanded clavicles and interclavicle are present, and limb-bones — very small — from the pectoral limb, indicating (as does the skull) aquatic habits. All in all, the evidence suggests that *Mytaras* was a Carboniferous ancestor of the larger and still more elongate Permian genus.

Archegosaurus

(Figs. 9, 13, 28)

A very different type of long-snouted rhachitome, although one developed from the same stage in temnospondyl evolution is *Archegosaurus decheni*, represented by numerous examples in nodules from the Lebach stage of the Lower Permian in the Saar. This was one of the first fossil amphibians to receive adequate description (at the hands of Meyer 1857); numerous further notes have been added by later writers, as Jaekel (1896) and most recently Whittard (1928) and Hofker (1928), (cf. Watson 1919, pp. 9–10).

Archegosaurus was, like *Chenoprosopus*, a long-snouted form (presumably a fish-eater), but unlike the latter genus in that the snout, although somewhat rounded terminally, was slenderly built; the general contours of the skull resemble those of the embolomere *Archeria* ("*Cricotus*"), an animal with presumably similar habits. In primitive fashion, the jaw condyles are far to the rear of the occiput. A long series of growth stages, showing increasing ontogenetic elongation of the snout, is known. The skull roof pattern is an elongate modification of the orthodox rhachitomous one; the nostrils have remained fairly close to the tip of the snout. In the larger individuals the lateral line grooves are in part visible.

In palatal view may be seen the movable, and hence persistently primitive, basal articulations and the occipital condyle, likewise primitive in remaining essentially a single structure, although with

emphasis, rather as in *Eryops*, on the exoccipital components. The elongate interpterygoid vacuities are rather narrow and the pterygoids

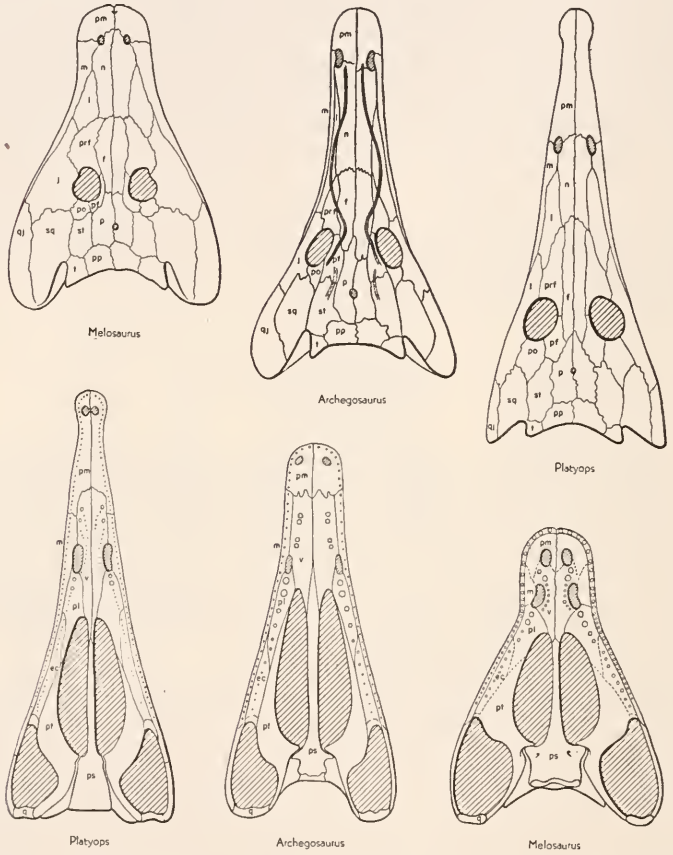

Fig. 28. Archegosaurids. *Melosaurus* after Meyer, Hartmann-Weinberg, Efremov; *Archegosaurus* after Burmeister, Meyer, Watson, Whittard; *Platyops* after Bystrow and Efremov (mainly *P. watsoni*; basal articulation from *P. stuckenbergi*).

extend forward nearly to their anterior ends. The choanae do not lie beneath the external nares, but are located much farther posteriorly, so that an elongate nasal channel was formed and the premaxillae no longer enter the choanal borders (cf. *Lysipterygium*, *Micropholis*);

the *Chenoprosopus* structure may represent an intermediate morphological stage in this peculiar development. The pterygoids are denticulate. Some uncertainty appears to exist as to the dentition of the elongate vomers. As in several forms already discussed, and as in various stereospondyls, there has developed, on palatine and ectopterygoid, a longitudinal row of teeth of which the most anterior are by far the largest. There is a well developed retroarticular process on the long and slender mandible.[1] The postcranial skeleton is represented by a considerable amount of material, including remains of branchial bars, an elongate trunk and tail with typically rhachitomous vertebrae[2], much expanded dermal girdle elements, and small limbs.

Archegosaurus represents, it is reasonable to believe, a development parallel to *Chenoprosopus* from a similar ancestry. There is no strong reason to believe that *Archegosaurus* has developed through a broad-snouted stage such as is seen in that genus, and more probably it has developed directly from ancestors with a generalized skull shape.

"*Archegosaurus*" *ornatus* (Woodward 1905) is represented by two fragmentary specimens from Khunmu, Kashmir, in *Gangamopteris* beds apparently equivalent to those containing *Lysipterygium* (discussed above) and perhaps Lower Permian in age. The material includes impressions of much of the skull roof, although few sutures are visible. Due to the elongation of the skull, with a pointed snout, the species was assigned to the (roughly contemporaneous) *Archegosaurus*. This assignment is uncertain, for there appear to be considerable differences. Both snout and post-orbital regions are less elongate than in the European form, and the lateral line grooves are more conspicuous.

Platyops

(Figs. 3, 12, 28)

This genus, known from three species (*rickardi*, *stuckenbergi*, and *watsoni*), is a common form in zones I-III of the Russian continental Permian (Twelvetrees 1880; Trautschold 1884, pp. 10–27, pl. 5; Efremov 1933; Bystrow 1935, figs. 26, 32a). *P. rickardi* and *P. stuckenbergi* are from zones I and II in the current nomenclature of

[1] As Nilsson notes (1944, p. 52), Whittard's restoration of the inner surface of the jaw (1928, fig. 2b) may be subject to revision.

[2] Jaekel (1896, fig. 5) shows a caudal vertebra with both "interdorsals" and "interventrals", instead of the typical rhachitome pleurocentra. I suspect, however, that these supposedly separate elements are merely two sections through the pleurocentrum (cf. his fig. 4).

the Russian continental Permian, the Kazanian stage. They were described in earlier decades and are represented by incomplete remains. *P. watsoni*, recently described, is founded on a large suite of materials from Upper Permian limestones on the Wjatka River, presumably from a higher horizon, zone III. A definitive account has not yet appeared.

The dorsal skull roof shows a still more elongate variant of the pattern seen in *Archegosaurus*, from which *Platyops* is reasonably believed to have descended. The snout region is proportionately about one-third again as long as in the earlier genus. The external nares, however, have failed to keep up, so to speak, with the process of elongation, and are no farther forward proportionately than they were in *Archegosaurus*; the snout is tipped by a pair of much elonagte premaxillae. The later forms of the genus are said to be more elongate than the earlier. The palate is likewise comparable to that of *Archegosaurus* in most regards. The development of the interpterygoid vacuities is similar; the pterygoids still extend well forward laterally. The choanae are, as in *Archegosaurus*, oval in outline and although again well in advance of the level of the interpterygoid vacuities are (as in that genus) distinctly posterior to the external nares. The major elongation of the snout is formed, below as above, by the premaxillae alone. Pterygoid as well as parasphenoidal body are denticulate; palatine and ectopterygoid have a tooth arrangement similar to that of *Archegosaurus*. The vomer bears a tusk-pair from which extends, as in many labyrinthodonts, a row of smaller teeth running back medial to the choana and a second row curving back toward the mid-line.

The construction of the basicranial region is of particular interest. The jaw articulation is approximately at the level of the skull condyles and skull table margin. However it is difficult to interpret this condition as due to forward movement of the articulation. If ventral views of *Archegosaurus* and *Platyops* are compared, it will be seen that the construction of the upper jaw region is identical in the two; there has been no abbreviation of the quadrate ramus of the pterygoid or shifting of this structure to a transverse position. Instead, there appears to have been a marked elongation of the region of the braincase posterior to the basal articulation. In this process there is a great longitudinal expansion of the parasphenoid. The body of this bone, as Efremov notes, is comparable to a shovel blade; the exposed surface is flattened; on either straight lateral margin the surface curves upward parallel to the adjacent pterygoid. The bone is ex-

tended posteriorly so as to conceal ventrally the ossified occipital region.

In *P. stuckenbergi* the basal articulation is still movable; in *P. watsoni*, according to Efremov's statement and Bystrow's diagrammatic figure, pterygoid and parasphenoid are immovably united.[1] A full account of *P. watsoni* is eagerly awaited; a major change of this sort is hardly to be considered intra-generic in nature.

The occiput is relatively high and narrow; the supraoccipital region is unossified, the basioccipital somewhat reduced, so that distinct exoccipital condyles are developing. As figured by Efremov in *P. stuckenbergi*, the opisthotic extends the length of the paroccipital bar and there is no development of a descending flange of the tabular. The opisthotic ossification extends well forward, without indication of suture, around the fenestra ovalis, but there are no indications of more anterior ossifications in the braincase. A foramen within the exoccipital is interpreted as for the vagus.

In the elongate jaws, the symphysis is, as might be expected, extremely long. Described postcranial structures are few, but as far as they go appear to be comparable to those of *Archegosaurus*. The vertebrae are typically rhachitomous but with a tendency toward fusion of elements in old individuals.

It is reasonable to believe that *Platyops* is a descendant of *Archegosaurus* or of a related form. The possible significance of the genus in connection with the ancestry of the trematosaurs will be discussed in connection with that group. Ecologically, the discovery of the *P. watsoni* materials in a limestone deposit may be significant in connection with the possible marine environment of the Trematosauridae.

Melosaurus

(Fig. 28)

The type specimen of *M. uralensis*, consisting of the skull and jaws, was discovered a century ago in the upper copper-bearing sandstones of the Kazan region of the west Urals — Zone II of the current Permian nomenclature — and described by Meyer (1860a). No other specimens have been positively identified, but Efremov has

[1]In Figure 28 the anterior portion of the palate is copied from Bystrow's figure; the region of the articulation is from *P. stuckenbergi*.

described further material as belonging to this or a closely related genus.

Two recent attempts at restoration of the *Melosaurus* skull have been made, by Efremov (1937) and by Hartmann-Weinberg (1939). The latter's restoration was made from a new preparation of the type skull; as Hartmann-Weinberg notes, Efremov's description of the palate was based on the non-typical material noted above, in which the palate resembles that of *Benthosuchus* and other neorhachitomes and appears, as regards the region of the basal articulation, markedly dissimilar to the type.[1]

In most respects the skull roof is that of a normal rhachitome which, however, is distinguished by elongation of a narrow snout, strongly suggesting a stage in the development of the features seen in *Archegosaurus* and *Platyops*. The external nares have, however, remained far forward and are of small size.

Much of the palate and occiput, newly prepared, is described by Hartmann-Weinberg. The occipital condyle is apparently advanced to the typical rhachitomous condition; the exoccipitals are prominent in its formation, the basioccipital reduced. On the other hand, the basal articulation, as in the genera just described, is of the primitive, freely movable type. Palatal vacuities are rather modestly developed and the cultriform process of the parasphenoid is slender. Paired anterior palatal vacuities are present. The arrangement of the palatal teeth is similar to that seen in *Platyops* and probably present in *Archegosaurus*.

In *Melosaurus* we see, as in the forms just described, the development of a slender-snouted type in a relatively primitive stage of rhachitome evolution. There is no reason to believe that there is any particularly close relationship between *Melosaurus* and *Chenoprosopus*; the nature of the skull elongation is rather different in nature. Hartmann-Weinberg argues for close relationship to *Archegosaurus*. That genus was earlier in appearance and yet longer-snouted; however, she believes that the present specimen is immature and that in the adult the snout would have been more elongate. It seems reasonable to believe that there is an actual relationship here, and it is possible that *Melosaurus*, even if mature, may be a persistently primitive archegosaurid.

[1]But compare our remarks on the basal articulation in *Platyops* from earlier and later zones.

Cacops

(Figs. 12, 13, 29)

From this excursion into the more primitive micropholoids, we return to a consideration of the remaining eryopsoid families. *Cacops* is in most regards the best known member of the Family Dissorophidae, a specialized side-branch of the typical rhachitome stock abundant in the Lower Permian of North America. All described remains of *C. aspidephorus* (Williston 1910) are from a single small pocket in the Clear Fork Group of the Lower Permian of Texas.

Like other dissorophids, *Cacops* was an amphibian of modest size, with a skull length of about 15 cm. The skull is remarkably high with nearly vertically placed cheeks. From above, the skull contours are, superficially, of the "central" labyrinthodont type, although the orbits are prominent, as one would expect in a relatively small form, and the face is rather short. The external nares are rather large, and placed more anteriorly and closer to one another than in most rhachitomes. The most striking specialization is seen in the otic region. The otic notch is greatly exaggerated. It extends forward two-thirds the distance from the end of the skull table to the orbit, and expands ventrally and posteriorly in the direction of the quadrate region, bounded below by a broad inturned bony rim. This great opening is, however, closed behind in *Cacops* by a bar of dermal bone descending from the tabular region to the quadrate. An enclosed otic notch is present in a few other labyrinthodonts apart from dissorophids; never, however, does the notch assume the relatively large size seen here.

The sutural pattern has not been made out on the skull roof; presumably, as in *Broiliellus* (described below), it was for the most part of a normal rhachitomous type.

The palate is well preserved in *Cacops*, although unfortunately sutures are not visible. The slender cultriform process of the parasphenoid separated large interpterygoid vacuities. The basal articulation was immovably fused; the area of union of parasphenoid and pterygoid was of the proportions seen in *Eryops*. The subtemporal vacuities extended far forward, and the pterygoid developed a definite projecting flange. The forward extent of this latter element is uncertain. The choanae are elongate ovals. The palatine bears a typical tooth-and-pit structure, the vomer a fang (an accompanying pit was not observed); no tusk was seen in the ectopterygoid region.

In the braincase, a sphenethmoid was ossified, but this was apparently separated by an unossified gap from the more posterior ele-

ments, of which little is known. The condyle has advanced far toward the tripartite condition, although the two exoccipital surfaces are close to one another.

Except for details of the feet, the postcranial region is nearly completely preserved, and in many features indicates that *Cacops* was essentially a terrestrial animal; the dissorophids apparently represent a peak in the development of land life in the labyrinthodonts. The body was short and stocky, with but 21 presacral vertebrae, two sacrals — a remarkable feature for an amphibian — and a short tail of perhaps 21 or 22 segments. The vertebrae are rhachitomous. An unusual feature is the development of dermal armor in the form of

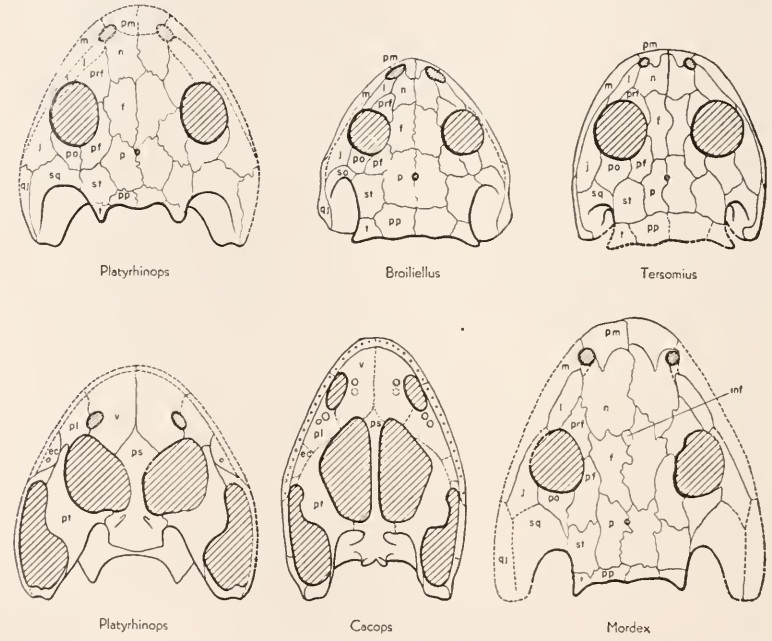

Fig. 29. Eryopsoids: dissorophids and *Mordex*. *Platyrhinops*, *Mordex* after Steen; *Broiliellus*, *Cacops* after Williston.

a connected series of transverse growths capping the neural spines, lying superficially in the dermis (as indicated by sculpture), and underlain by an expansion of the spine itself. Such beginnings of a

dorsal armor are present in a number of other Permian reptiles and amphibians as a defense against carnivorous synapsids, developed by the early Permian. The dermal plates were presumably continued laterally by a tough leathery hide, but there is no trace in the material of ossicles which might have been present in other parts of the potential carapace.

The limbs and girdles are stoutly built although, in correlation with the relatively small size of the animal, the limb elements are slender compared with those of contemporary eryopsids. The dissorophids were capable of terrestrial existence and probably had as little to do with the water as (for example) a bufonid toad of today. The scapulocoracoid was fully ossified (as a single element) and surmounted by a well developed cleithrum; clavicles and interclavicle were relatively little developed and unsculptured ventrally; the small interclavicle had developed a short posterior stem. The pelvis (including pubis) was fully ossified, the ilium short vertically and modestly expanded into a blade. The humerus is of the tetrahedral type, with a large deltopectoral crest, but with the supinator process not separated from the ectepicondyle. In the femur there is little development of a fourth trochanter and none of the external (posterior) proximal branch of the ventral crest system; the adductor crest is a single long high ridge terminating distally beneath the ectepicondyle. The external longitudinal ridge on the tibia is highly developed, as in *Zatrachys*.

Alegeinosaurus

The described remains of *A. aphthitos* consist merely of a partial skeleton, headless, from the Texas Clear Fork (Case 1911, pp. 60–62, fig. 12). The dorsal armor and such elements of the appendicular skeleton as are present greatly resemble the contemporary *Cacops*, but the thoracic ribs bear "uncinate" processes, not reported in that genus.

Dissorophus

This amphibian is likewise from the Clear Fork beds of Texas, (Williston 1910a; Case 1911, pp. 115–119, fig. 45); *D. multicinctus*, *D. articulatus*, *Otocoelus testudineus* and *O. mimeticus* are in all probability cospecific. The genus is certainly closely related to the contemporary *Cacops*, as Williston notes, and Efremov (1937, p. 25) has suggested that the two are growth stages of the same animal.

However the major part of the material of both consists of individuals of approximately the same size, and yet exhibits the features contrasting the two genera. In *Dissorophus* the dermal armor is more expanded, a fused shield is developed over the "cervical" region, and the limbs are more stoutly built.

Broiliellus

(Fig. 29)

Closely related to the last two genera is *B. texensis*; this form is, however, distinctly more primitive in certain regards, and was earlier in appearance, suggesting that it was ancestral to the Clear Fork genera. The type (Williston 1914) is from the Clyde Formation of Texas, a horizon transitional between the Wichita and Clear Fork groups; specimens of this or some closely related genus are found from this point downward to the Putnam Formation of the Wichita.

Broiliellus, in known specimens, is rather smaller than the typical Clear Fork dissorophids, and is much shorter-faced. The otic notch is, as in those forms, enormously developed, and the tabulars curve laterally toward the quadrate region. These processes, however, do not close the otic notch as in *Cacops* and *Dissorophus*.

In this genus, fortunately, most of the sutures on the skull roof are visible. The pattern is, as expected, of the general rhachitomous type. However the lacrimal extends the full distance from naris to orbit, and the frontal enters the orbital margin — features associated with large orbital dimensions. Further, the expansion of the otic notch is associated with a marked reduction of the surface exposure of the squamosal, at the expense of which enlargement has occurred; this element, however, appears to form much of the flange of bone within the lower margin of the notch.

The palate, as far as exposed, agrees with that of *Cacops*, but the marginal areas are not visible. There is a well developed series of supra-vertebral dermal plates, much as in *Cacops*, but the neural spines themselves are not expanded. Such limb and girdle material as is known is similar to that of *Cacops*.

Probably to be assigned to this genus is "*Aspidosaurus*" *novomexicanus* of the New Mexican Abo (Lower Permian) (Williston 1911, pp. 12–13, pl. 38, fig. 1; Case and Williston 1913). The short face of this open-notched dissorophid is comparable to that of *Broiliellus* rather than *Aspidosaurus*, and the age of these New Mexican beds is comparable to the Wichita, in which *Broiliellus* is found, rather than the Clear Fork.

Tersomius

(Fig. 29)

The only specimen of *T. texensis* (Case 1910, pp. 180–181, fig. 10) is a small skull, about an inch in length, from the Lower Permian Wichita Group of Texas. The skull is short and broad, and it has been suggested that *Tersomius* is a "branchiosaur", i.e., a young individual of some sort of rhachitome. That it is juvenile is suggested by the fact that many of the cranial elements had become partially separated along the lines of suture before burial.

Only the skull roof is visible. The orbits are large, in part at least in correlation with small absolute size; the lacrimal enters both orbit and naris; the jugal barely reaches forward below the orbit. The nares are somewhat more medially placed than in typical rhachitomes. The area of the squamosal is much reduced, apparently by forward encroachment of the otic notch. These are dissorophid features; and particularly diagnostic is the nature of the otic notch itself. This is very large, and extends downward to a very low level on the side of the cheek; and it is bounded anteriorly and ventrally by a strongly inturned flange of the squamosal, in typical dissorophid fashion.

Tersomius has been described as having a short skull table, with short postparietals and little, if any, trace of tabulars, a condition quite unlike the dissorhophids. But examination of the type shows that the supposed posterior end of the table is an eroded surface, not a natural one, and we may confidently restore a table of dissorophid type. The skull is very similar to that of the contemporary *Broiliellus* and may be that of a young individual of this animal. If so, it will be noted that the present name has priority.

Aspidosaurus

A. chiton (Broili 1904, pp. 40–44, pl. 6) is a Clear Fork dissorophid, the type material of which consists of a skull and fragmentary postcranial material. The skull is visible only from the upper surface. It is rather more elongate facially and closer to the central rhachitomous shape than either *Broilliellus* or *Cacops*. It is, unfortunately, imperfect; sutures are not seen, and while there was obviously a large otic notch, its posterior portion is missing. There are rhachitomous vertebrae which dorsally bear narrow, roof-shaped, sculptured ex-

pansions which show no indication of separation from the neural spines. Thus *Aspidosaurus*, despite its relatively late date, is a more primitive member of the family than either of the two genera last described.

Several other species have been assigned to this genus. *A. glascocki* (Case 1910, pp. 179–180, fig. 9) of the Wichita of Texas is based on vertebrae which are dissorophid, and appear to show a narrow dorsal shield in which successive segments are fused, but the specimen is doubtfully referable to this genus. *A. crucifer* from the Wichita of Texas is based on a neural spine of the *Zatrachys* type, as is *A. apicalis* of New Mexico. "*A.*" *novomexicanus*, likewise from the Lower Permian (Abo) of New Mexico, is, as noted above, closer to *Broiliellus*, and *A. peltatus* of Texas is probably incorrectly referred.

Zygosaurus

The type of *Z. lucius* was an incomplete skull from the Russian Permian, discovered and described nearly a century ago (Eichwald 1848, pp. 159–202, pls. 2–4) and since lost; it has been recently discussed by Efremov (1937, pp. 24–26, fig. 4, pl. 3). The type was from the lowest continental Permian of Russia (Zone I); Efremov (1940, p. 378) notes, however, similar remains from Zones II and III.

As first pointed out by Watson (1919, p. 8), *Zygosaurus* is very similar, as far as can be told, to the dissorophids, and especially to *Cacops*, in general topography and (particularly) in the closure of the otic notch. Efremov suggests that it might even be a member of the same genus. *Zygosaurus* was the last of the dissorophids.

Platyrhinops

(Fig. 29)

This Carboniferous amphibian is known only from imperfect skull material from the Westphalian of Linton, Ohio, and was based generically by Steen (1931, pp. 865–867, figs. 11–13) on the poorly known "*Tuditanus*" *mordax* of Cope. The skull pattern is in general that of typical rhachitomes, but the shape is rather short and broad. The anterior end and lateral margins are not preserved. Although the orbits are widely separated, the frontals come very close to their margins, suggesting dissorophid conditions. Strongly suggesting such

assignment is the development of enormous otic notches, which extend far forward toward the orbits, reduce the squamosals markedly, and allow the supratemporals to enter broadly into the medial margin of the openings. The pointed tabulars suggest the initiation of the characteristic development here in advanced dissorophids. However, the skull table is not as elongate as in some later dissorophids, and the jaw articulation is hence well back of the region of the occiput. An odd feature is that the large frontals extend back to the neighborhood of the pineal opening.

On the palate, the interpterygoid vacuities are broad, the vomers greatly expanded. The pterygoid and parasphenoid were unquestionably firmly united. The lateral margins of the palate are mostly obscured by the jaws. A small ectopterygoid tusk is visible, but such structures were not seen on palatine or vomer. Almost the entire palatal surface is covered by a shagreen of small teeth, and much of the area of the interpterygoid vacuities appears to have been covered by a series of small dermal "bonelets" bearing similar teeth — a feature also seen in the contemporary *Stegops*. The braincase is not preserved.

Like so many of its Linton fellows, *Platyrhinops* was believed to be a phyllospondyl, and related to *Stegops*. The latter genus is, however, now known to be a rhachitome, and *Platyrhinops*, despite the lack of vertebral material, is surely a member of that group. Further, such features as the loss of the intertemporal and fusion of the basal articulation show that it is by no means a primitive rhachitome but one on the level of development of the *Eryops* group. Still further, the otic notch structure very strongly suggests that we are dealing with a Carboniferous ancestor of the Permian dissorophids.

Arkanserpeton

A small femur from the Pennsylvanian of Arkansas described by Lane (1932) is the only material of *A. arcuatum*. The Paris shale, in which the specimen was found, contains a typical Westphalian flora, comparable to that of the lower Allegheny. The femur, with a well-developed unbranched adductor crest, is comparable to that of the dissorophids, with which it may be very tentatively placed. We have noted above the presence in the Pennsylvanian of a possible precursor of this typically Permian family.

Trematops

(Figs. 12, 30)

Another family of early Permian rhachitomes which had progressed far toward a terrestrial existence, and one which exhibits many resemblances to the dissorophids, is that of the Trematopsidae, of which *Trematops* is the typical genus. *T. milleri* from the Texas Clear Fork beds was first described by Williston (1909); Olson (1941) has recently redescribed this and other trematopsid remains on the basis of a considerable amount of material collected by the Harvard and Chicago University museums. A second species, *T. thomasi*,[1] from approximately the same horizon in southern Oklahoma (Mehl 1926), Olson notes, is indistinguishable from the genotype. A further Texas species, *T. willistoni*, was described by Olson.

The outlines of the *Trematops* skull are of the generalized eryopsid type, but the otic notch extends far forward toward the orbit, and the skull is relatively high and narrow. The jaw articulation is well back of the occiput. A small median opening, perhaps for a gland, is present between the premaxillae (and nasals). A characteristic specialization is the great posterior elongation of the external nares. This has been thought to lodge a gland, but Olson believes this improbable. Behind the naris the lacrimal broadly enters the orbital margin and restricts the usual forward extension of the jugal. As in dissorophids, the frontal enters the orbital margin. A second major peculiarity is the great size of the otic notch, developed here to much the same degree as in the dissorophids so that it excises much of the squamosal and, bordered by an internal bony flange, descends diagonally backward and downward to the quadrate region. The tabulars are greatly produced in horn-like fashion outward and downward and in *T. milleri* (but not in the species illustrated) reach the quadrate and close the otic notch posteriorly.

The palatal elements show for the most part a generalized and rather primitive condition. Few sutures are visible, but the pterygoids certainly extended forward nearly to the anterior end of the interpterygoid vacuities, which are unusually small for an advanced rhachitome. The cultriform process of the parasphenoid is very slender as in primitive forms but, in contrast with most rhachitomes, extends forward above the plane of the vomers. The choanae are

[1]Kuhn (1933, p. 68) states in error that the type is at the University of Missouri; it forms part of the collections of the University of Oklahoma.

elongate slits, and there is a medial anterior palatal opening just back of the premaxillary tooth row at the bottom of a deep depression in the vaulted vomers. The palate is definitely advanced in the fusion of pterygoid and braincase, although the area of junction is slender.

Except for a gap between sphenethmoid and otic region, the braincase is well ossified; there is even ossification in the supraoccipital region which, however, is covered by strong descending flanges of the dermal elements above. The condyle consists of two strongly developed circular surfaces, presumably mainly on the exoccipitals, which are closely appressed. From the parasphenoid there is developed a marked pair of basisphenoidal tubera. The lower jaw was slenderly built and appears to have had but a single splenial. There are no symphysial tusks on the dentary.

Most of the postcranial skeleton is adequately known. In the vertebral column the intercentra are greatly developed, and Olson notes that in *Trematops* (although not in *Acheloma*) they may extend upward to surround the notochord, thus showing parallelism to the embolomeres on the one hand and to the stereospondyls on the other. The girdles and limbs are well developed and well ossified, and strongly indicative of terrestrial habits. In many features, such as the pelvic structure, nature of the femoral trochanteric system etc., there are marked resemblances to the dissorophids; there are, however, certain differences (such as the presence of a small supinator process on the humerus)[1]. As in dissorophids, clavicles and interclavicle were very small. Carpus and tarsus were well ossified, and there is a nearly complete hind foot (formula 2.3.3.4.2), most recently discussed by Schaeffer (1941).

Trematops thus presents a mixture of primitive, advanced and specialized features. In general palatal construction there are primitive characters, particularly in the small size of the vacuities. The rather high and narrow skull and nonplatybasic structure of the sphenethmoid region are presumably primitive, as is the generally high degree of ossification of the braincase. On the other hand, fusion of the basal articular region, loss of the intertemporal, and subdivision of the condyle are all advanced features indicating a typically rhachitomous grade of organization. It is not impossible, however, that some of the features of this grade were attained by the trematopsids independently of the typical eryopsids, and that the trematopsids are thus a development parallel to that group.

[1]The humerus often figured as that of *Acheloma* is not associated.

Peculiar to *Trematops* and its close relatives is the diagnostic specialization of the narial region. In many other regards, as Olson recognizes, they are strikingly suggestive of the dissorophids. In the skull the comparison is close between the development of the great otic notch in the two groups, and even to its complete closure in extreme cases. The skulls are different in appearance, due in part

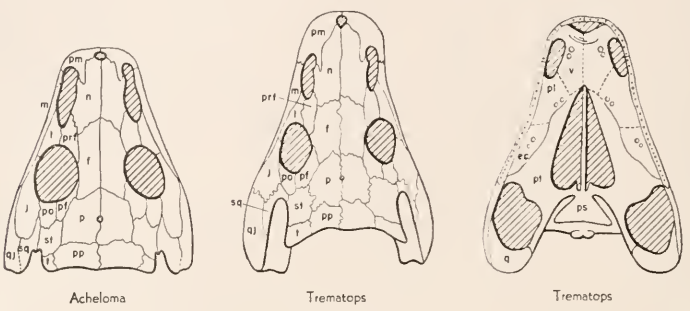

Fig. 30. Trematopsids. Mainly after Olson.

to the usual shortness of the face in dissorophids; but between *Trematops* and the relatively long-faced *Aspidosaurus* the contrast is much less marked. In the postcranial skeleton the similarities are numerous and striking. Much of the resemblance between the families may be laid to parallelism, as Olson suggests; but resemblances are so numerous that it is not improbable that there is a real relationship, and that the parallelism is true parallelism, in the narrow sense of the term, between closely related evolutionary phyla.

Acheloma

(Fig. 30)

Long obscure, the nature of this Texas Lower Permian genus (cf. Case 1911, pp. 34–37, 104–106, pl. 11) has been revealed by recently discovered material (Olson 1941); it proves to be a genus close to *Trematops* but rather more primitive in nature. The genotype, *A. cumminsi*, is recorded as occurring in the Clear Fork, but this may be inaccurate, and two new species erected by Olson (*A. pricei, A. whitei*) are from the Wichita beds (Putnam and Belle Plains Formations, respectively). These forms differ from *Trematops*, among

other features, in the shorter muzzle anterior to the external nares, in the much slighter degree of development of otic notch specialization, and in a tendency for less perfect ossification of the postcranial skeleton. The genus is presumably ancestral to *Trematops*.

Parioxys

This poorly known genus (cf. Case 1911, pp. 32–33, fig. 4) was described by Cope on the basis of two skulls from the Wichita of Texas. It was suggested by its describer that *Parioxys* was the young of *Eryops*, and immature specimens of that genus have been identified as *Parioxys*. As Case notes, however, the two are quite distinct. This amphibian is represented in the Harvard collections by the remains of several individuals; unfortunately they were embedded in a difficult matrix, little of which has as yet been removed. The skull has much the proportions of *Trematops*, but lacks the peculiar narial opening of that genus. The otic notch was certainly well developed, but details of its construction are obscure. As in *Trematops*, the jaw ramus is slender. The postcranial skeleton, as far as prepared, shows various features comparable to those of the *Trematops* group and to the dissorophids; most noteworthy is a development of "stereospondylous" intercentra as in *Trematops*. It is concluded that *Parioxys* is related to and probably to be included in the Trematopsidae, representing a primitive stage in which narial specialization is not apparent. In this respect, at least, the genus approaches somewhat more closely the dissorophids. However, if, as suggested above, the dissorophids were already beginning their development in the Westphalian, *Parioxys* is very late in time to be considered as a form close to the common ancestry of the two families.

Mordex

(Fig. 29)

With considerable doubt *M. calliprepes* (Steen 1938, p. 260, fig. 42) from Nýřany may be suggested as a possible predecessor of the trematopsids. This is known only from a single example of the skull roof, incomplete as to its margins. The pattern is that of a typical rhachitome in which the intertemporal is lost, but there is no way of judging whether, for example, the genus still retained movable palatal articulations or had fused them in eryopsid fashion. There is a tiny

interfrontal. Other features, equally unimportant, suggest comparison with the trematopsids: comparable development of the premaxillae, with a posterior process; entrance of lacrimal into the orbital margin. Perhaps significant, however, is the structure of the otic notch region. This structure is of a size unequalled in any Carboniferous rhachitome with which I am familiar except the presumed dissorophid *Platyrhinops*; the supratemporal is broadly exposed on its upper border, and the pointed tabulars emphasize its extent, as in trematopsids. This evidence, slight as it is, suggests provisional association of *Mordex* with the Trematopsidae.

Acanthostoma

(Fig. 31)

Apparently widespread in the early Permian, but not too well known as to structure, is a family of rhachitomes, the Zatrachydidae, of which *Acanthostoma* of the Niederhässlich deposit of Saxony is morphologically the best known; the data have been reviewed by Steen (1937), following earlier description by Credner (1883, pp. 277–289, pls. 11,12) and by Geinitz and Deichmüller (1882, pl. 7, figs. 8, 9). Some eight specimens of *A. vorax* are known, all of small size, and ranging in skull length from about 12 to 80 mm. The smallest are obviously larvae. The largest has been tacitly assumed to be adult; but since the remains of large individuals of any type of tetrapod are rare at this locality, it may well be that the true adult was still larger in size; as will be seen, much larger members of the group are present in other Permian localities.

In many regards the skull roof of *Acanthostoma* is that of a normal, moderately advanced rhachitome. The jaw articulation has moved forward to about the level of the occiput. The skull is very flat and broad. The sutural pattern is for the most part that found, for example, in the contemporary eryopsids, but the lacrimal is primitive in its retention of orbital contact. There are, however, very distinctive features. The premaxillae and nasals are large, and the "snout" much expanded; between these two pairs of elements is a large opening, perhaps associated with glandular development. A second characteristic feature is the development of a spiked "frill" on each quadratojugal, which may be interpreted as a defensive structure. The tabulars are somewhat projecting, but not to any marked degree.

On the palatal surface, the interpterygoid vacuities are broadly rounded, but their considerable development is overshadowed by the expansion of the lateral and (particularly) anterior areas of the palate; the vomers are of extremely large size. Between these elements and the likewise expanded premaxillae, and underlying the opening on the upper surface, is a large palatal vacuity. In the general fashion of advanced types, the cultriform process of the parasphenoid is rather flattened and articulates anteriorly between the vomers. Most of the palate is covered by a shagreen of small denticles and there are, in addition, the three normal pairs of tusks on either side.

Some doubt exists as to the nature of the basal articulation. Steen notes that in the smaller skulls of the series available to her, the basipterygoid processes end in smooth articulating surfaces, whereas Jaekel's restoration (1911, fig. 127, etc.) figures a sutural connection. As pointed out elsewhere, determination of the true nature of the articulation in immature individuals is often problematical; the existence of a sutural union in the related genus *Stegops* suggests that such a condition was also present in the adult *Acanthostoma*.

The braincase (including occiput) is, unfortunately, unknown and obviously was poorly ossified in these little animals. The jaw had a slender ramus and is noteworthy in that the angular, like the quadratojugal above it, carried a spiked frill. The smaller specimens show traces of ossified branchial arches.

A few limb and girdle bones are present, but show little in the way of distinctive characters. Until the publication of Steen's 1937 paper, only the neural arches were known to be ossified in the vertebral column, and both she and the writer believed *Acanthostoma* to be a "branchiosaur". As always, this has proved to be false; for she finds ossified rhachitomous central elements in the largest specimen of the series. She interprets these structures as including paired intercentra as well as paired pleurocentra. However neither her descriptions nor figures suggest that the intercentra were of a nature other than that found in normal rhachitomes. Thus the intercentra which are shown in her figure 4, no. 5, are apparently such structures seen in ventral — not lateral — view.

Zatrachys

(Fig. 31)

An American contemporary and relative of *Acanthostoma*, but an animal of much larger size than any known specimen of that genus,

was *Zatrachys* of the Lower Permian Wichita and Clear Fork Groups. A number of skulls and partial skulls are known, but the structure is imperfectly understood. There are three described species: *Z. microphthalmus*, *conchigerus* and *serratus*, doubtfully distinct. The roof has been best figured by Broom (1913, pp. 592–595, fig. 21). The general characteristics are those already seen in *Acanthostoma*, but

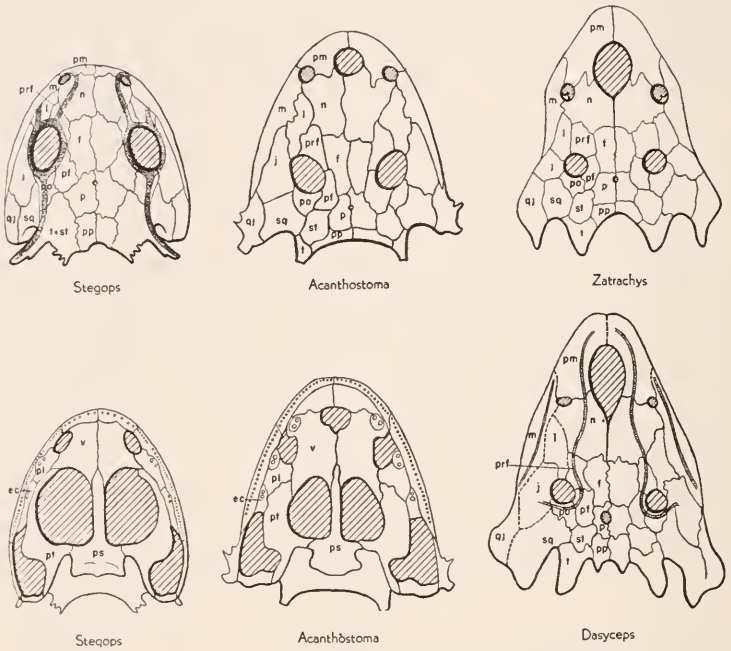

Fig. 31. Zatrachydids. *Acanthostoma* after Steen; *Stegops* after Romer, Steen; *Zatrachys* after Broom; *Dasyceps* after Huene.

with exaggeration of the peculiar features of that type. The rostral region is still more expanded anterior to the nares and the broad nasals, and the rounded dorsal opening of *Acanthostoma* is further enlarged as an oval slit. A great swollen flange of bone takes the place of the more modest serrate quadratojugal of *Acanthostoma*, and the tabulars are here much elongated. A partial palate (Case 1911, fig. 43A) closely resembles that of *Acanthostoma*. The occiput is comparable to that of *Eryops*, but more flattened, and the two condyles are more distinct than in that type.

No articulated skeleton is known, but a number of limb bones of distinctive character may be associated with a fair degree of certainty. Unquestionably (as proved by *Platyhystrix*, *vide infra*) *Zatrachys* possessed a unique type of neural spine which has been found isolated in the Wichita beds and sometimes assigned to this genus, sometimes to *Aspidosaurus* as *A. crucifer*. These spines terminate, as in dissorophids, with a transverse sculptured plate. In some instances (as Case 1911, fig. 15C) the spines are low, and the capping plates keeled after the fashion of a house roof; in others, in which the spine is much elongated and flattened, the sculptured area descends far down on either lateral surface. No such structure is reported in *Acanthostoma*. In one instance typical rhachitomous central elements have been found associated with the *Zatrachys* type of spine.

Platyhystrix

Closely related to *Zatrachys*, if not identical, is *P. rugosus* of the Abo (Lower Permian) of New Mexico. This genus was founded on the basis of long spines which were reasonably assumed to belong to a pelycosaur analogous to *Dimetrodon* or *Edaphosaurus* in the development of a "sail" (a shorter spine had been earlier named *Zatrachys apicalis*). These spines, however, were later discovered to be associated with a skull very similar to that of *Zatrachys* (Williston 1916a, pp. 204, 206, fig. 45). The skull is imperfect, but is obviously of the general *Zatrachys* type. The spines are not in series and the longitudinal distribution of low and high types is unknown. Obviously, however, we have an example of the development among amphibians of a "sail" in the fashion of contemporary pelycosaurs. This development of a vertical body flange is even more unexpected than in other groups because of the great flattening seen in the cranial region.

Dasyceps

(Fig. 31)

The one large zatrachyid (with a skull length of 39 cm.) known from Europe is the type skull of *D. bucklandi* from the Lower Permian of Kenilworth, England (Huxley 1859a), best described by Huene (1910). As may be seen from the figure, this specimen exhibits the same general features as *Zatrachys*, but the rostrum, median fenestra

and posterior projections are even more pronounced than in the Texas form. However the generic nature of these distinctions is questionable; possibly *Zatrachys* and *Dasyceps* are synonymous. Again it is quite possible, considering the disparity in size, that *Dasyceps* is the truly adult form of *Acanthostoma*.

Stegops

(Fig. 31)

The grotesque type of structure seen in the Permian zatrachyids is one which would be expected to develop at a late stage in the evolution of progressive rhachitomes. It was therefore astonishing to find in *Stegops divaricata* of the Westphalian cannels of Linton (Romer 1930, pp. 114–118; Steen 1931, pp. 860–865, figs. 8–10) an amphibian in which the specializations of the group were already far advanced. There were, as yet, neither dorsal nor ventral fenestrae in the rostral region, nor any expansion of the premaxilla; the preorbital region was, in fact, rather short. The nasals above and the vomers below were, however, already well expanded. There was no expansion in this genus of the flange of the quadratojugal seen in later genera, but the tabular-supratemporal region was greatly developed, and, as in *Acanthostoma*, the angular region of the jaw was flanged.

The skull bears a series of rounded ridges which (in contrast to the usual amphibian condition) appear to have enclosed lateral line canals. Tabular and supratemporal appeared to be fused in the material available to me. The basal articulation was closed by suture. As in *Acanthostoma*, the palatal dentition included not only normal tusk-pairs but a widespread shagreen of denticles. As in *Platyrhinops* this denticulation appears to have covered the area of the interpterygoid vacuities, supported by a mosaic of flat ossicles.

Both the writer and Steen believed *Stegops* to be a "phyllospondyl". Since this animal is very similar to *Acanthostoma* and to *Zatrachys*, this led the writer to the logical but absurd conclusion that the latter, a large amphibian, which was generally regarded as a rhachitome (although vertebrae were then unknown), was an overgrown branchiosaur, and drove Steen to the belief that *Stegops* and *Zatrachys* were unrelated. However, we now know rhachitomous vertebrae in *Zatrachys* and *Acanthostoma*, and Steen has described in *Stegops* wedge-like vertebral structures which are presumably rhachitomous intercentra.

DISCUSSION

In this section I have treated of a very considerable series of genera which in various diagnostic characters are seen to pertain broadly to the typical rhachitome group, typified by *Eryops*. All have palatal vacuities of rather large size; all have lost the intertemporal element; most have at least begun the subdivision of the occipital condyle leading to the bipartite structure of the later Triassic labyrinthodonts.

We have noted, however, that certain forms appear to be on a somewhat more primitive level of organization than the characteristic eryopsids, particularly as regards the retention of a movable articulation between palate and braincase. Certain of these forms — *Potamochoston*, *Lysipterygium* — are poorly known, rather "synthetic", and it is not impossible that they are immature specimens of animals which had a sutural union here as adults. Others, however — *Micropholis*, the long-snouted *Archegosaurus*, *Chenoprosopus* and their relatives — appear to be definitely members of this rather transitional category. It is not impossible that future early Pennsylvanian discoveries may give further rhachitomes of this description. We here distinguish this more primitive group, systematically, from the more advanced genera which constitute the main bulk of the material considered, as the Superfamily Micropholoidea; the eryopsids and related families constitute the Eryopsoidea.

In earlier decades the Rhachitomi were considered to be characteristic only of the Permian; few if any were thought to have come into existence before the close of the Carboniferous. We have already noted the occurrence in the Pennsylvanian of a number of primitive rhachitomes. In the present section it has been seen that the evolution of the group had progressed very far during that period; the "flowering" of the group took place in the early Permian, but all the essential features of the more typical Rhachitomi were developed in Pennsylvanian times, and numerous phyletic lines were distinguishable in the Westphalian and Stephanian. Obviously rhachitomes were common inhabitants of the coal swamps. Most striking is the appearance in the Westphalian of such advanced and specialized types as the first of the Zatrachydidae and, apparently, of the Dissorophidae.

Admitting the imperfection of our knowledge, some attempt may be made to outline a provisional framework of a classification and phylogeny of the micropholoids and eryopsoids. Seemingly the most primitive of the Micropholoidea are *Lysipterygium* and *Potamochoston* which, if they prove not to be larvae of more progressive types, may

constitute the Lysipterygiidae. *Micropholis* appears to be a late-lingering form of the same sort, but is perhaps sufficiently specialized to be regarded as typical of a separate family. From more generalized micropholoids may have been derived two long-snouted families, the Archegosauridae (*Archegosaurus, Platyops, Melosaurus*) and Chenoprosopidae (*Chenoprosopus, Mytaras*).

A supposed central stock of the more progressive Eryopsoidea is that represented by *Eryops, Onchiodon, Actinodon, Sclerocephalus, Chelydosaurus* and *?Osteophorus*, with the typical "branchiosaurs" for the most part furnishing evidence as to their larval history. These are the classic rhachitomes of the early Permian. Watson (1919) would subdivide this group into two families, at least, on the basis of clavicular development. To the writer, however, it seems more useful to emphasize the essential similarity of (for example) *Eryops* and *Actinodon* than to stress their relatively slight differences, and I therefore include them all in the Eryopsidae.

Most of the remaining genera of eryopsoids can be reasonably arranged in three families: Dissorophidae (*Cacops, Alegeinosaurus, Dissorophus, Broiliellus, Tersomius, Aspidosaurus, Zygosaurus, ?Platyrhinops ?Arkanserpeton*); Trematopsidae (*Trematops, Acheloma, ?Parioxys, ?Mordex*); and Zatrachydidae (*Zatrachys, Acanthostoma, Platyhystrix, Dasyceps, Stegops*). These families flourished in the early Permian, and it might be reasonably concluded that they had sprung from the Eryopsidae at a date not much earlier. Here, however, we encounter the fact that there are no surely known eryopsids before the Permian, whereas these seemingly specialized families of eryopsoids were apparently started on their careers in the Pennsylvanian — one of them, at least, and perhaps two, as early as the late Westphalian. It is not at all impossible that the Eryopsidae evolved at a relatively late date and that these other forms had arisen independently and earlier from the edopsoids or the transitional micropholoids. We may further note the fact that there is suggestive evidence that these three families are actually related. We have commented on the resemblances between dissorophids and trematopsids; and there are suggestive similarities between *Stegops*, first of the zatrachydids, and the contemporary *Potamochoston*, seemingly an early dissorophid.

The suggestion of independent development of eryopsoid families from the more primitive stocks brings into sight the spectre of parallelism, always lurking in the background in any discussion of amphibian evolution. It is quite possible that the Eryopsoidea are

polyphyletic in origin, but this is not necessarily true, and until such a case is proven, we may reasonably regard them as a systematic unit.

Watson has pointed out the fact that in the typical rhachitomes we see the peak of development of terrestrial life in the labyrinthodonts, in contrast to the primitively aquatic embolomeres and the presumably secondarily aquatic stereospondyls. The Eryopsidae, with stoutly built limbs, are definitely well toward the terrestrial side of amphibious life; the dissorophids are even more markedly terrestrial in adaptations, and the trematopsids, too, are stout limbed. This trend toward land was not, however, a universal one. We have noted that even among the primitive rhachitomes, *Trimerorhachis* and similar types were already seemingly retrograde. On the micropholoid level, the long-snouted forms, as *Archegosaurus* and *Chenoprosopus*, are aquatic labyrinthodonts for which it is unnecessary to postulate a previous semi-terrestrial ancestry, and the zatrachydids seem to have been definitely aquatic.

TREMATOSAURS

Discussed here is a series of early Triassic labyrinthodonts, aquatic and presumably piscivorous, usually included in the Stereospondyli but now known to be rhachitomous in vertebral structure although advanced in other regards. These are here considered to constitute a separate suborder, the Trematosauria. Genera included are *Trematosaurus*, *Trematosuchus*, *Tertrema*, *Stoschiosaurus*, *Aphaneramma*, *Gonioglyptus*, *Platystega*, *Lyrocephalus*, *Peltostega* and *Rhytidosteus*.

TREMATOSAURUS

(Figs. 3, 9, 13, 32)

T. brauni is an "average" member of the group, and also merits consideration as one of the first of labyrinthodonts to become adequately known. Early descriptions of this form, from the Bunter of Bernburg, were given by Burmeister (1849) and Meyer (1858). Additions to our knowledge have been made by a number of later writers, including Watson (1919, pp. 38–41, figs. 23–25), Drevermann (1920), Huene (1920, pp. 442–444; 1921a), Jaekel (1922, pp. 18–20, figs. 6–8 etc.), Wagner (1935) and Säve-Söderbergh (1937, p. 194, fig. 4). "*Labyrinthodon*" *ocella* from Bernburg (Meyer 1855, p. 140,

pl. 61, figs. 1, 2) is known from a single incomplete and poorly preserved skull. It appears to show a curious and impossible mixture of trematosaur, capitosaur and "rhachitomous" features. One may suspect, as early suggested by Alberti (1864, p. 238), that it is a distorted specimen of *Trematosaurus*; Watson (1919, p. 41) notes a second specimen which may be of the same nature. *T. fuchsi*, from the Bunter of Kahla, Thuringia (Seidlitz 1920) is probably identical with *T. brauni* (Jaekel 1922, p. 7). *Trematosaurus* was reported from the Lower Triassic of Mt. Great Bogdo in southeastern Russia by Sushkin (1927, pp. 277–278, figs. 5, 7, 8) and Efremov (1932); the material is comparable to that of *brauni*. The genus is further cited from South Africa as *T. kannemeyeri* (Broom 1909, pp. 270–271; Haughton 1925, pp. 249–250), from the Upper Beaufort beds of the Orange Free State. This specimen has never been figured, and Huene (1920, pp. 446–447, fig. 8) considers that it is more like *Aphaneramma*; Watson suggests *Trematosuchus* (1919, p. 41).

The superficial cranial anatomy was adequately portrayed by Burmeister; Jaekel, Bystrow and others have later made useful restorations. The skull, about a foot in length, is slender, tapering to a point anteriorly so that the outline (repeated in other genera of the group) is essentially triangular. The orbits are at about the mid-point of the skull length so that not only is the face elongated but — unusually — the post-orbital region as well. A characteristic feature of the present group is the lateral position of the orbits. Unlike that of most of its Triassic contemporaries, the skull is not depressed; the height above a line through the quadrates is about half the total width, and the sides of the cheek region are nearly vertical, with the orbits facing as much laterally as dorsally; the long snout appears to have had an essentially tubular structure. The contours are comparable to those of *Archegosaurus* and *Platyops* amongst earlier temnospondyls and the *Pteroplax*-"*Cricotus*" group among embolomeres; a piscivorous mode of life is strongly suggested.

Lateral line grooves are well developed, confirming the other indications of aquatic habits. Their topography is a normal pattern, except for a tendency toward multiplication of grooves in the post-orbital-supratemporal region, and a separation of the supraorbital groove from the rest of the system.

Taking into account the elongation of the skull, the topography of the roofing bones calls for little comment; the arrangement of the elements is that of typical Permian rhachitomes. The palate is highly comparable in many ways to that of the neorhachitomes or capito-

saurids except for differences in proportions due to the length and slenderness of the skull. The cultriform process of the parasphenoid is very slender and separates large interpterygoid vacuities; the pterygoids have short palatal rami which fail to reach the palatines. There are paired anterior palatal vacuities. The tooth arrangement on the palate is highly comparable to that of the neorhachitomes except for the absence of small teeth between the vomerine tusk-pairs. The palate is also comparable anteriorly to that of *Archegosaurus* or of *Melosaurus* in many regards; we may note that those genera show a multiplication of palatal teeth comparable to that in *Trematosaurus*. The palatines are relatively short, the ectopterygoids elongated in this and other trematosaurs.

The construction of the basal articulation of palate and braincase, and the structure of the braincase, as seen in *Trematosaurus*, are repeated in other trematosaurs with little change. They may be described here with data gathered from *Lyrocephalus*, *Aphaneramma* and other genera as well as from *Trematosaurus*; Watson, Stensiö, Sushkin and Säve-Söderbergh (particularly the last) are the main contributors to our knowledge of the internal anatomy of the trematosaurid skull.

As in almost all temnospondyls beyond the earliest Permian, the basal articulation is immovable, and ventrally parasphenoid and pterygoid are broadly apposed. A somewhat similar development of an elongate parasphenoid-pterygoid contact has been attained by other Triassic temnospondyls, but in a different fashion. In them there appears to have been a gradual backward extension of an originally narrow line of union of pterygoid with braincase; when the length of the line of contact is increased, the pterygoid may become united superficially with the exoccipital; the parasphenoid does not tend to reach far back; there is frequently a retention of the basisphenoidal tubera, and the base of the occipital region is visible ventrally.

In trematosaurs, on the other hand, the parasphenoid has expanded far backward to the condyles as a flat plate ventral to the basicranial region, so that, apparently, the area of attachment of the ventral neck muscles lies in a slit dorsal to the posterior margin of the parasphenoid. In consequence of this posterior development of the parasphenoid, the posteriorly expanded pterygoid suture meets the parasphenoid throughout its course, although deep to this contact the pterygoid is also in apposition, to a slight degree, with the exoccipital.

As in other advanced temnospondyls, the broadened palatal articulation entirely conceals the course of the internal carotids. They pass forward in the cranio-quadrate passage beneath the posterior portion of the shelf formed by pterygoid and parasphenoid, and enter the substance of the latter bone in a pocket posterior to the basipterygoid process and below the fenestra ovalis. Canals for their progression medially and forward to their point of entrance into the braincase have been seen by Säve-Söderbergh. Paired foramina opening from the substance of the parsaphenoid into the posterior end of the interpterygoid vacuity are interpreted by that writer as for the palatine branch of the facial nerve. They are, however, more probably canals for the palatine artery branching from the internal carotid; a superficial groove on the pterygoid interpreted by Säve-Söderbergh as for this artery is presumably for minor superficial vessels. In the posterior part of the palato-quadrate complex, the quadrate ramus of the pterygoid is high but short. An area which may be associated with the middle ear cavity includes a "tympanic recess" ventrally, opposite the fenestra ovalis; it is bounded posteroventrally by a diagonal ridge on the medial surface of the pterygoid, anteriorly by a ridge descending the steep anterior margin of the quadrate ramus. At the upper end of this ridge the pterygoid appears to have gained a contact with the crista parotica.

The quadrate, as far as known, does not extend forward to any marked degree from the articular region. The epipterygoid was incompletely ossified. It has a broad ascending process slanting forward as well as upward toward the lateral wall of the "laterosphenoid" region of the braincase and is said to be fused to that area at its dorsal end. Posteriorly an ossified extension of the element runs upward in an otic process to gain contact with the parotic crest of the braincase. The ventral margin of the epipterygoid is irregular; its cartilaginous extension may have covered a considerable area of the lateral surface of the pterygoid.

On its medial aspect the pterygoid exhibits an elongate sutural surface for the parasphenoid (and exoccipital). An extension of this articular surface rises upward behind a deep pocket in the pterygoid termed the "conical recess". Comparison with *Eryops* and neorhachitomes shows that this branch of the articular area is homologous with that seen in more primitive forms behind the socket receiving the basipterygoid process of the basisphenoid, and it is obvious that the "conical recess" of the trematosaurs is this socket.

As compared with most Triassic temnospondyls, the trematosaur

braincase is relatively high and narrow. The supraoccipital area was unossified, and the basioccipital usually cartilaginous and at best weakly developed. However the exoccipitals were, as in temnospondyls

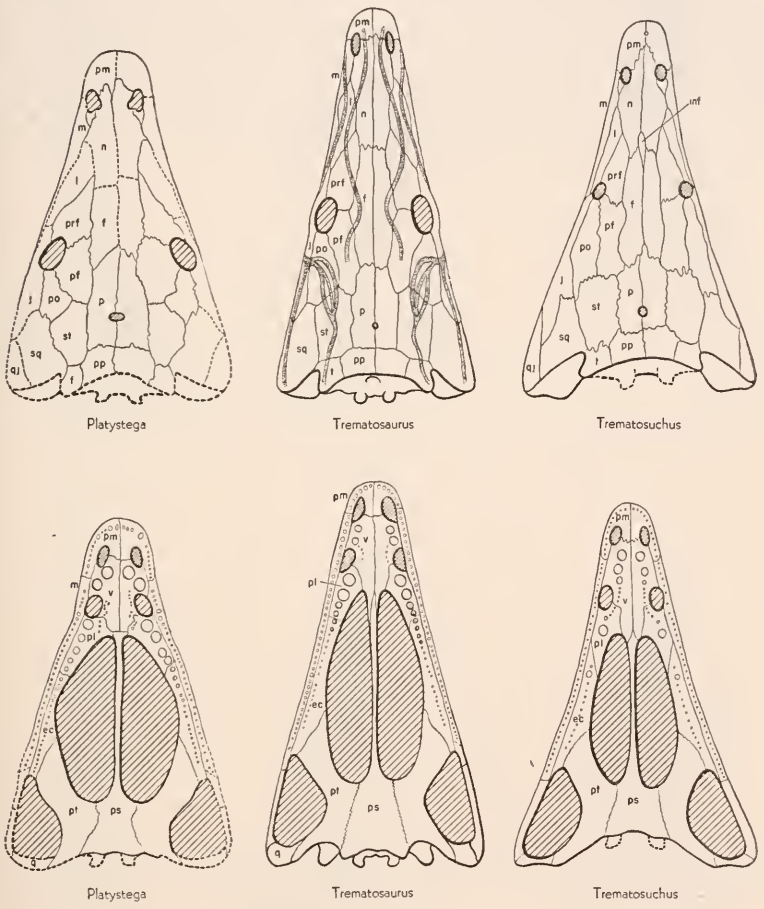

Fig. 32. Trematosaurs. *Platystega* after Säve-Söderbergh; *Trematosaurus* after Burmeister, Watson, Wagner, Bystrow; *Trematosuchus* after Haughton.

generally, highly developed. The condyles were paired, widely separated from one another and cartilaginous at their tips. Above, the exoccipitals met strong descending flanges from the roofing bones

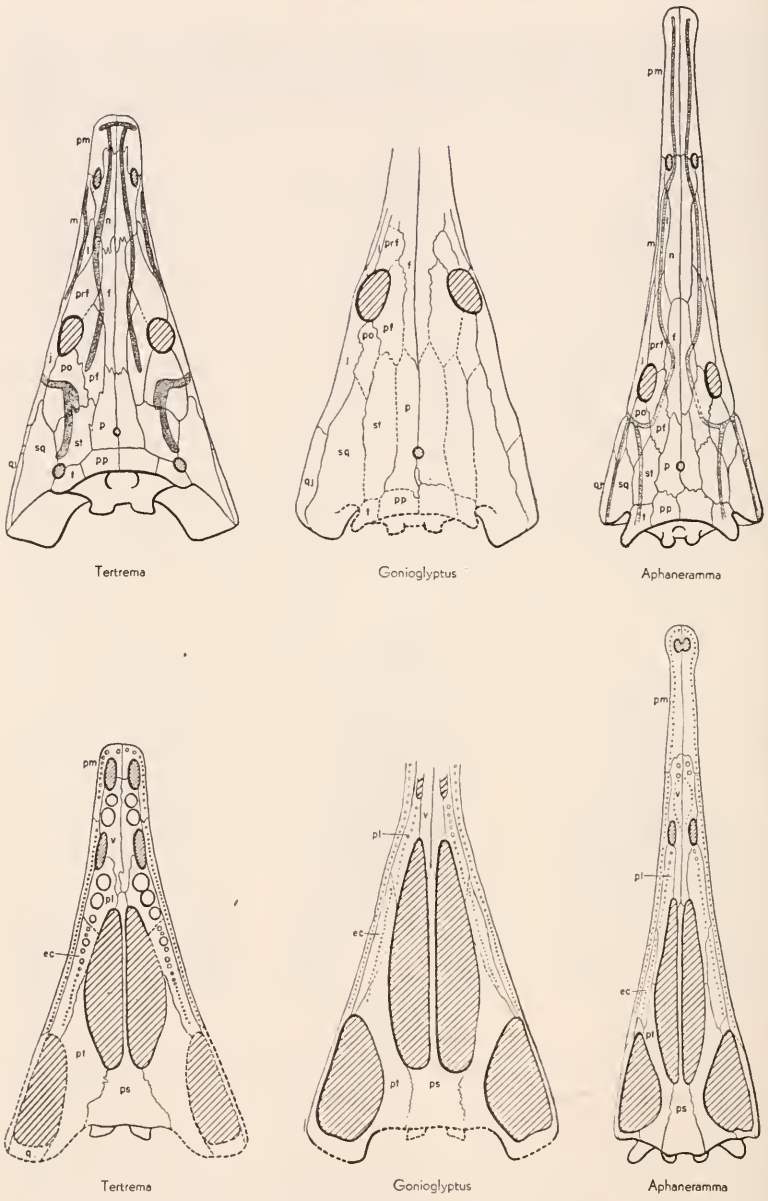

Fig. 33. Trematosaurs. *Tertrema* after Wiman, Säve-Söderbergh; *Gonioglyptus* after Huene; *Aphaneramma* after Wiman, Säve-Söderbergh, Bystrow.

— the postparietals medial to the well-exposed posttemporal fossae, the tabulars laterally. The opisthotics are eliminated from the posterior surface of the paroccipital bar, but presumably the otic capsule extended, as in all other known labyrinthodonts, well out into the paroccipital process anterior to the area ossified as the tabular; Säve-Söderbergh (1936, figs. 7, 38, etc.) assumes an unusual truncation. The exoccipital extends far forward along the lateral margin of the otic capsule to the region of the fenestra ovalis and gains a contact with the pterygoid in the floor of the cranio-quadrate passage.

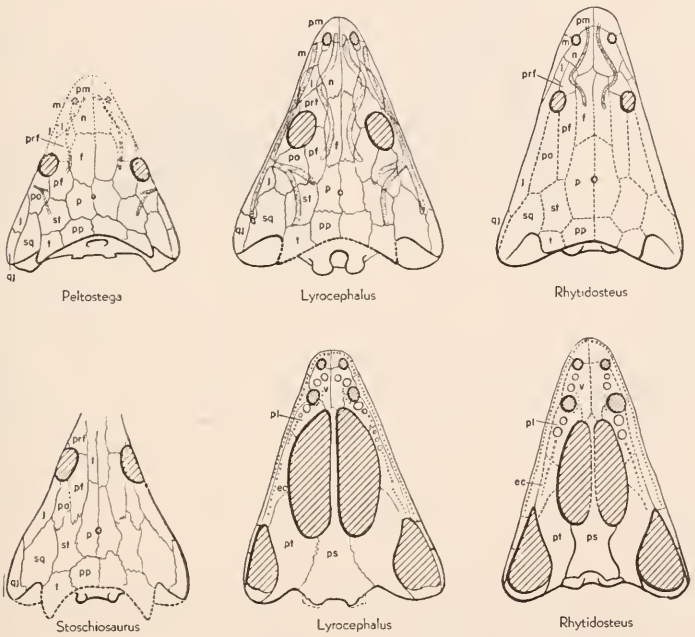

Fig. 34. Trematosaurs. *Peltostega*, *Lyrocephalus* after Wiman, Säve-Söderbergh; *Rhytidosteus*, composite restoration after Owen, Haughton; *Stoschiosaurus* after Säve-Söderbergh.

The braincase is very feebly ossified in the anterior portion of the otic capsule region and that of the basisphenoid, and the lack at that time of adequate knowledge of the braincase of more primitive amphibians appears to have led Säve-Söderbergh in 1936 to a reconstruction which seems surely erroneous in various major respects.

A prootic ossification is seen lying above the fenestra ovalis and extending upward to the parotic crista, partially surrounding the opening of the posttemporal foramen and running backward into the posttemporal fossa. The inner anterior margin of this element presumably formed the outer wall of a depression in which, as in *Eryops*, lay the ganglia of the trigeminal nerve. Posterior to the prootic, the opisthotic is feebly ossified and usually purely endochondral; in one specimen of *Aphaneramma*, however, it is developed perichondrally in the region above and behind the fenestra ovalis.

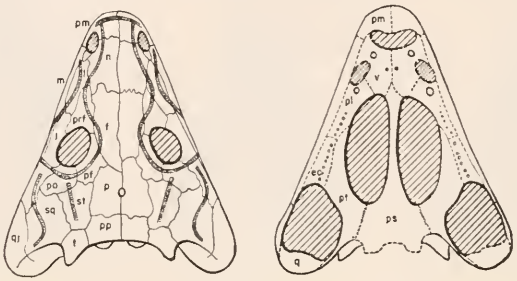

Fig. 35. *Lyrocephalus* (?) from East Greenland. After Säve-Söderbergh.

The basisphenoid region remains unossified or at best only feebly ossified in specimens identified as trematosaurid, but enough ossification is occasionally present to show the existence of the canal and recess posterior to the pituitary which carried the "pituitary" interorbital vein and lodged eye musculature in *Eryops*. A braincase most recently described by Säve-Söderberg (1944), but not identified taxonomically, shows most of the outline of this opening.

Postero-ventral to this opening we find in primitive temnospondyls and all anthracosaurs a stout projecting basipterygoid process received into a socket in the pterygoid and epipterygoid; this is one of the most important landmarks in the topography of the braincase. This process is still present in such typical rhachitomes as *Eryops* even though the joint is a fixed one. Säve-Söderbergh has assumed that this process was reduced in trematosaurs to a slender connection between sphenethmoid and epipterygoid (1936, fig. 12, *pbt*, *prb*). It seems, however, that it was unquestionably present and typically developed here, although in cartilaginous rather than osseous form, as the "core" of the braincase-palatal articulation. We have noted the typical socket for its reception. Its position on the lateral surface

of the braincase can be determined from the fact that the ascending ridge of the parasphenoid, present just behind the process in *Eryops*, is duplicated by a similar ridge in trematosaurs. And finally, Säve-Söderbergh shows in excellent photographs (1936, pl. 7, fig. 1, *rc*; 1935, pl. 5, fig. 2, *p*), the exact shape of this process in the form of the matrix replacing the process in the "conical recess".

In the anterior part of the braincase there is a well-developed sphenethmoid, described particularly by Säve-Söderbergh. Posteriorly the ossification is usually poorly developed, so that generally the "laterosphenoid" region was at least partly cartilaginous. It seems certain, however, that this area was solidly constructed in life, as in primitive temnospondyls, and the greater part of this area is ossified in the recently described specimen noted above.

The jaw is, as expected, slender anteriorly. The dentary bears a stout pair of symphysial tusks and smaller supplementary teeth. Posteriorly the jaw deepens and there is a very highly developed retroarticular process. As far as can be seen the bony elements are of fairly normal arrangement, but not all the sutures are certain. There is a curious dearth of postcranial material — indeed, the same is in general true of all trematosaurids. In the rich Bernburg material there are only a few elements which have ever been described as possibly belonging to this form. Burmeister and Meyer figured dermal shoulder elements which, as expected, are elongated antero-posteriorly, and the former figured three other bones, one of which may be a scapulocoracoid. Nothing is known in this genus of vertebrae, ribs or limbs.

Trematosuchus

(Fig. 32)

The genus was erected by Watson in 1919 (p. 41) for a skull from the Lower Triassic *Cynognathus* zone of South Africa which Haughton (1915a) had described as *Trematosaurus sobeyi*. As Haughton indicates, in a description of the type and a second skull in 1925 (pp. 250–253, figs. 15, 16), the supposed generic characters were mainly due to the incomplete preparation of the specimen at the time of original description. The form is clearly a trematosaurid and on the whole fairly comparable to *Trematosaurus*. There are, however, various differences which appear to make a generic distinction valid. The pre-narial region of the snout is more developed than in *Trematosaurus*; the orbits as figured are very small; the lacrimal is described as reach-

ing the orbits. Certain of these features may, of course, be due, again, to imperfect material. An interesting detail is the presence of an interfrontal, as in *Eryops*, *Kestrosaurus* etc.

Tertrema

(Fig. 33)

T. aeuta is known from two incomplete skulls from the Eotriassic of Spitzbergen, described by Wiman in 1915 (p. 21, pl. 6, fig. 7, pl. 7, fig. 1) and 1917 (pp. 229–237, figs. 1, 2, pls. 11–13) and commented on briefly by Säve-Söderbergh in 1936 (pp. 112–114, figs. 50, 51). The two specimens supplement one another, so that skull roof and palate are adequately represented. *Tertrema* is clearly a trematosaurid, comparable in most ways to *Trematosaurus*, but with a rather more elongate and slender snout, suggesting a trend toward the exaggerated *Aphaneramma* condition. A specialization is a closing of the otic notch posteriorly, comparable to that seen in several other, unrelated labyrinthodonts. The snout is very slender, but the anterior vacuities remain separate. The vomerine and palatine fang-pairs are very large, and no smaller teeth are reported on the vomers. To *Tertrema* is assigned, with doubt, an incomplete dermal girdle (Nilsson 1943a, pp. 235–236).

Stoschiosaurus

S. nielseni was described by Säve-Söderbergh in 1935 (pp. 140—150, figs. 57—59, pls. 4, 5, 15, fig. 2) on the basis of an internal cast of a skull, lacking the snout, from the Eotriassic of East Greenland; several other similar specimens were referred to this genus. The dermal bone pattern of the post-orbital portion of the skull roof is clearly seen (although the fact that the bones themselves are absent deprives us of knowledge of the sculpture or lateral line grooves) and the posterior part of the palate is present. Some internal features of the skull are available and are described; they are trematosaurid in nature. The form is clearly a trematosaur with a much elongate, triangular-shaped post-orbital region. The general proportions, as Säve-Söderbergh notes, suggest a comparison with *Aphaneramma* (and *Gonioglyptus*). His suggestion that the genus is morphologically ancestral to *Aphaneramma* is a reasonable one; we cannot, of course, be sure how far the present genus had gone in snout elongation.

Aphaneramma

(Figs. 12, 13, 33)

The first amphibian described from the Eotriassic of Spitzbergen was *A. rostratum* of Smith Woodward (1904), based on an incomplete skull of a very long-snouted amphibian. Wiman in 1910 gave the name of *Lonchorhynchus öbergi* to a skull fragment. To *Lonchorhynchus* was assigned further material described by that author in later years (1915, pp. 14–20, figs. 7–8, pls. 3–5; 1916, p. 220, fig. 4, pl. 16, fig. 2; 1917, p. 238, fig. 8, pl. 13, fig. 5). This form had an elongate skull, but the snout was incompletely represented and relationship with *Aphaneramma* was unsuspected. The relationship was realized, however, by Smith Woodward, and the identity of the two was confirmed by Säve-Söderbergh, who has redescribed the "*Lonchorhynchus*" material (1935, p. 139, fig. 56; 1936, pp. 58–112, figs. 24–49, pl. 12, figs. 2–4, pls. 13–16, 17, figs. 1, 2, pls. 18–21; and 1937, pp. 195–199, figs. 5–8).

The genus is a spectacularly long-snouted modification of the trematosaur type. The post-orbital region in itself is much elongated, the region between orbit and nares still more elongated, and anterior to the nares the premaxillae project far in advance (the exact length of the "rostrum" is conjectural). In every structural feature, however, *Aphaneramma* is clearly a trematosaurid, despite its grotesque proportions, and one which can be readily derived from a *Trematosaurus*-like form, with *Tertrema* and *Stoschiosaurus* representing intermediate morphological stages in elongation.

Palatal modifications in the main are those expected in such an extremely elongate skull. The anterior palatal vacuities at the tip of the slender snout have fused into a single opening, and the choanae are far removed from the tip. The vomerine and palatine tusk-pairs are greatly reduced, but rows of smaller teeth persist on the vomers and more posterior elements. In contrast to the situation described in other trematosaurs, the palatine sends back a long extension medial to the ectopterygoid and persistently maintains a contact with the pterygoid.

Considerable data are available on internal cranial construction (Säve-Söderbergh 1936); the general pattern is that described under *Trematosaurus*. The slender jaw has been described by Nilsson (1943, pp. 5–18, figs. 2–9; pls. 1–3, pl. 4, figs. 1–4). The stapes (Säve-Söderbergh 1936, pp. 109–110, fig. 47 etc.) is notable for the presence of a dorsal process. *Aphaneramma* is one of the few members of the

group in which associated postcranial material of any sort is available (Nilsson 1943a). In one specimen associated clavicles and interclavicle are present. The interclavicle is shaped much as in *Trematosaurus*, but, as expected, rather more elongate in contour, with a long slender anterior process flanked by the clavicles (which do not meet) and a long posterior extension. The same specimen also shows poorly preserved remains which include scapula, humerus, and ribs, and Nilsson describes another humerus, radius and ulna.

Smith Woodward described several vertebral centra from the same locality as the *Aphaneramma* type, but these are presumably ichthyosaurian. Nilsson, however, (1943a, pp. 254–260, figs. 11–14) shows that *Aphaneramma* had a "neorhachitomous" type of vertebra, with intercentra well-developed, but pleurocentra apparently unossified. Welles (1946) notes the presence of an *Aphaneramma*-like form in the Moenkopi of Arizona.

Gonioglyptus

(Fig. 33)

G. longirostris was described by Huxley (1865, pp. 3–5, pl. 6) on the basis of a skull fragment from the Panchet group of the early Triassic of India; Huene more recently (1920) assigned to the same genus, as *G. kokeni*, a second skull which includes a nearly complete post-orbital region, this from the *Prionolobus* beds of the Lower Triassic of the Salt Range of the Punjab. The two together give us a fairly adequate knowledge of skull roof and palate, except for the snout and the posterior margin of the skull table. As Huene notes, we are dealing with a trematosaurid, and one which in general compares with *Aphaneramma*. The rostral region was undoubtedly long, although its exact nature is uncertain; the post-orbital elements are even more attenuate than in the contemporary Spitzbergen form. Huene believes an intertemporal to have been present, but the evidence is not altogether satisfactory. Huene's specimen shows a small "centroparietal" (as does also one individual of *Aphaneramma*). As in most trematosaurs, the palatine is not in contact with the pterygoid. The distance, shorter here than in *Aphaneramma*, between choanae and interpterygoid vacuities, suggests that *Gonioglyptus* had a less elongate snout.

A number of other, isolated specimens from the Panchet may pertain to *Gonioglyptus*. Huxley assigned to the genus a slender jaw

with a long retroarticular process. *Glyptognathus fragilis*, based on a specimen which Lydekker (1882, p. 27, pl. 1, fig. 1) supposed to be the greater part of a jaw of distinct type, appears to be merely part of a dentary which may be that of a *Gonioglyptus*. *"Gonioglyptus" huxleyi* of Lydekker (1882, pp. 26–27, pl. 1, figs. 5, 8) is the posterior part of a much larger jaw, probably belonging to *Pachygonia*. Lydekker assigns to *Gonioglyptus*, with doubt, an isolated jaw symphysis (1882, p. 27, pl. 1, fig. 6). Possibly pertaining to *Gonioglyptus* is a clavicle of reasonable size and proportions (Huxley 1865, pl. 6, fig. 8).

Platystega

(Fig. 32)

Having described the long-snouted variants of the trematosaur pattern, we may turn to others with shorter skulls but with the same basic triangular type of trematosaur skull. *P. depressa* is known only from a single skull from the Eotriassic of Spitzbergen, described by Wiman in 1915 (pp. 20–21, pl. 6, figs. 5, 6), and further described by Säve-Söderbergh in 1935 (p. 136, fig. 62) and 1936 (pp. 46–57, pls. 10, 11, 12, fig. 1). While both pre-orbital and post-orbital regions are somewhat elongated, the elongation is less marked than in *Trematosaurus* and still less marked than in the other genera earlier noted. The skull, too, is relatively broad posteriorly, but is markedly constricted anteriorly, to end in a slender snout; this is somewhat in contrast to the regular triangular shape usual in the family (but cf. Nilsson 1943, p. 26). The skull is preserved as a nodule from which the bones have been eroded, so that sculpturing and lateral line grooves cannot be determined. However, most of the sutures are clearly visible. Both dorsally and ventrally the structure is readily comparable with that in other trematosaur genera. Säve-Söderbergh has described a number of features of internal structure which can be made out in the posterior portion of the skull, and which are of a pattern comparable to those of other trematosaurs. Apart from the skull, Nilsson (1943a, pp. 234–235, fig. 5, pl. 1, fig. 1) has described a partial dermal girdle which may be that of *Platystega*.

Lyrocephalus

(Figs. 5–8, 12, 34, 35)

A common trematosaur from the early Triassic of Spitzbergen is *L. curi*, known from a number of skulls described by Wiman and later

writers in various papers (Wiman 1914; 1915, pp. 10–14, pls. 1–3; 1916, pp. 216–219, pl. 16, figs. 3, 4; Stensiö 1921, p. 141, pl. 20; Sushkin 1927, p. 278, figs. 9, 10; Säve-Söderbergh 1935, pp. 160–161, fig. 61; 1936, pp. 8–46, figs. 1–17, pls. 1–9, 12, 20–22; 1937, pp. 191–195, figs. 1–3; Nilsson 1943, pp. 18–23, figs. 10–12, pls. 4, 5). *Lyrocephalus* is a short-faced trematosaur, essentially similar to *Trematosaurus* in every feature: triangular, tapering skull shape; relatively high skull, rounded in section; laterally placed orbits; well-developed lateral-line grooves; broad articulation between pterygoid and elongate parasphenoid; slender cultriform process of the latter bone; similar palatal tooth arrangement; similar build of the anterior portion of the palate; various details of the internal anatomy of the skull.

It differs primarily from *Trematosaurus* in that the skull is only two-thirds as long, proportionately to its width, and that in consequence all the structures of the skull (except those at the far posterior end) are much different in their proportions. In many regards *Platystega* shows a half-way stage between the two.

A number of features of the internal structure of the skull are known in *Lyrocephalus*, and have been noted by Wiman and Stensiö and described in considerable detail by Säve-Söderbergh in 1936. Similar features are known to a greater or lesser degree in *Trematosaurus*; the general discussion under the former genus includes the *Lyrocephalus* data. The posterior part of the lower jaw is known (Nilsson 1943, pp. 18–23, figs. 10–12, pl. 4, fig. 5, pl. 5). The stapes lacks the dorsal process seen in *Aphaneramma*.

Of postcranial materials, Nilsson (1943a, pp. 232–234, 260–263, figs. 3, 4, 15, 16, pl. 1, figs. 2–4, pl. 3, figs. 4–5, pl. 4, figs. 2–6) has described dermal shoulder elements and vertebrae. The vertebrae are of a typical rhachitomous pattern, with well ossified pleurocentra of good size and essentially comparable to those of *Eryops* of the Permian.

Säve-Söderbergh (1935, pp. 150–183, figs. 60, 61, 63–66, pls. 7–13) has described from the Eotriassic of East Greenland a number of specimens, which he assigned to *Lyrocephalus* as *L. kochi*, *L. johanssoni*, *L. rapax* and *L. sp.* (Fig. 35). As Efremov has pointed out (Efremov 1940, p. 94; Bystrow and Efremov 1940, p. 100), these specimens are difficult to include in the genus *Lyrocephalus*. They have a triangular-shaped skull, rather as in that genus, but the snout is broader, the orbits are relatively more posteriorly placed, the lateral line grooves show a different arrangement, the anterior palatal vacuity is single rather than double; the pterygoid, as restored, reaches forward to

the palatine, etc. Efremov even goes so far as to suggest that these "*Lyrocephalus*" specimens are not trematosaurs, but members of the *Benthosuchus* group. Unfortunately the posterior part of the palate, which might yield decisive information, is unknown.

Peltostega

(Fig. 34)

This genus is known only from the holotype of *P. erici* from the Lower Triassic of Spitzbergen described by Wiman in 1916 (pp. 210–216, pl. 15, figs. 1–3, pl. 16, fig. 1). This consists of the post-orbital portion of a skull of considerable size for a trematosaurid (the width across the quadrates is approximately a foot). The dorsal surface is beautifully preserved and shows with great clarity a skull which is relatively short in the post-orbital region and tapers evenly forward toward the orbits. The anterior part of the skull is unknown, but on the assumption that the contours of the cheek were continued forward unchanged, Wiman has restored the form as extremely short-snouted.

The roof pattern is of normal type and quite comparable, on the whole, to that of *Lyrocephalus*, except that the post-orbital region is not elongated to even the mild degree seen in that genus, and the pineal opening is rather anteriorly placed; the extreme lateral position of the orbits is very suggestive of trematosaur conditions. The occiput shows a structure comparable to that of trematosaurs and is in contrast to that of metoposaurids and capitosaurids in that it is little depressed. The palate is poorly preserved. Wiman figures a part of the cultriform process of the parasphenoid as a broad structure which contrasts with the narrow ventral edge of this process seen in the typical trematosaur skull. Obviously, however, the specimen is badly eroded (part of the parasphenoid has disappeared completely) and it is probable that we are viewing not the ventral flange of the cultriform process but the base of the broader sphenethmoid which lay above it (cf., for example, Säve-Söderbergh, 1936, fig. 7).

There is no unanimity of opinion regarding the phylogenetic position of *Peltostega*. Smith Woodward in his 1932 revision of the Zittel text (p. 216) places it in the Metoposauridae, with doubt; I can see little resemblance in this genus to metoposaurids except the fact that the face was probably short. Säve-Söderbergh would place it in a distinct family because of the (doubtfully) broad parasphenoid and the slightly

different position of the pineal. There is little reason here for the erection of a new family. In almost all its features *Peltostega* seems clearly to be a good trematosaurid, but one in which the skull is shorter, to a modest degree, than in the undoubted trematosaurid *Lyrocephalus*.

Rhytidosteus

(Fig. 34)

One of the earliest fossil amphibians to be described from the Karroo beds of South Africa was *R. capensis* Owen (1884) from Beersheba, O.F.S., a locality which lies in the upper part of the Beaufort series (?*Cynognathus* zone) and hence is early Triassic. The type consisted mainly of the antorbital portion of a skull, showing a well-preserved dermal roof and a somewhat imperfect palate. Owen believed the skull to have been short post-orbitally. Watson (1919, pp. 35–36, fig. 21) described several fragments associated with the type but neglected by Owen. As well as giving some data regarding internal structure, they showed that, contrary to Owen's belief, the posterior portion of the skull must have been very elongate (and that in consequence Owen's assumption that one jaw ramus was complete is incorrect — the ramus as figured is quite short).

Haughton in 1925 (pp. 253–256, figs. 17, 18) based *Microposaurus casei* upon a skull from the Lower Triassic *Cynognathus* zone of Wonderboom, C.P. The general shape is elongate and triangular in outline, with the orbits far forward. This immediately suggests a comparison with *Rhytidosteus*, a form of similar size, definitely with similar skull proportions and probably from the same horizon. Unfortunately the skull sutures are not known in Haughton's specimen. I have attempted a composite restoration of the roof by using the *Microposaurus* outline, inserting upon it the known structures of the *Rhytidosteus* snout and restoring the post-orbital region in normal labyrinthodont fashion. In the *Microposaurus* type the orbits and nares appear to be more medially placed than in *Rhytidosteus*. This is seemingly due to the greater flattening of the skull in the former specimen. The general appearance thus given is in most aspects that of a trematosaurid, with the short face of *Lyrocephalus* or *Peltostega*, but with a greater elongation of the post-orbital region toward the conditions seen in *Trematosaurus* or, better, *Trematosuchus*. This discordant development of anterior and posterior segments is exceptional for trematosaurs.

The trematosaurid nature of this form — if the two be accepted provisionally as identical — is further confirmed by the palate of Haughton's specimen. In all its features it is closely comparable with those of trematosaurs. Many of these features, it is true, are also to be found in capitosaurids, but the excessively long slender corpus of the parasphenoid with its elongate suture with the pterygoid is not met with in that group as now known, nor is the excessive length of the parasphenoid-pterygoid contact found in capitosaurs until the later Triassic.

There are, however, disturbing points. Watson notes in a fragment of the type the absence of a hypoglossal foramen in the exoccipital, although this is reported in other trematosaur genera, and figures the exoccipital as seen in contact with the pterygoid in ventral view, whereas this contact is normally concealed ventrally in trematosaurs. However, one may hopefully believe these conditions as due to weathering of the fragment (which I have not studied). The skull described by Haughton appears to show the quadrate region extending far back of the occiput. Such a situation is not found in any trematosaur; nor is it, indeed, seen in any post-Carboniferous labyrinthodont of any sort; this appearance is presumably due to the distortion which, Haughton notes, the skull had undergone. The choanae, as figured by Owen and by Haughton in the two specimens, are quite different in shape; the slit-like appearance in the *Rhytidosteus* type may be due to lateral compression.

DISCUSSION

In the ten genera discussed above we have a group of forms which despite superficial diversity exhibit a long series of common features which strongly indicate that they are a natural unit, the Family Trematosauridae. Eight of the ten are certainly related; *Rhytidosteus* is perhaps doubtful because of inadequate knowledge; *Peltostega* is unusually short-faced, but otherwise well merits inclusion.

All have pointed triangular skulls, although the shape of the triangle varies from one with a very acute apex and narrow base in *Aphaneramma* to an almost equilateral condition in *Peltostega*. The skulls are relatively high and rounded, in contrast to typical Triassic labyrinthodonts, with the orbits facing as much laterally as dorsally. Lateral line grooves are well-developed, indicating aquatic habits in the adult; the suborbital groove lacks the abrupt "jog" upward

into the lacrimal seen in most other forms in which these grooves are well developed. The palate is to some extent distinctive; a long corpus of the parasphenoid makes a very broad contact laterally with the pterygoid, and extends back to end in a transverse shelf just anterior to the condyles; the exoccipital-pterygoid contact is not visible ventrally. There is a long slender parasphenoidal rostrum; a "pinched" vomerine region; a series of palatal teeth comparable in most points to those of the neorhachitomous genera, but tending generally to a greater development of tusks anteriorly; anterior palatal vacuities accommodating symphysial tusks of the lower jaw. The occiput is relatively high and narrow, with distinct exoccipital condyles and the exclusion of the much reduced opisthotics from a superficial position on the occipital surface. A seemingly characteristic series of internal structures is noted in the description of *Trematosaurus*. The lower jaw is slender, particularly anteriorly, and with a powerful retroarticular process.

The general impression of habitus given by the skull features is that of a group of active piscivorous water dwellers. As regards the postcranial skeleton, our data, as was seen, are meager. Such endochondral bones as are preserved are poorly ossified, a fact which in itself is strongly suggestive of aquatic habits. The few limb elements are small and weak, again indicating a water dwelling existence. One may reasonably assume a long, slim body shape, paralleling that of fish eaters of the *Cricotus* group among embolomeres and of *Archegosaurus* among earlier rhachitomes. The elongate interclavicle of *Aphaneramma* suggests such a bodily elongation in some, at least, of the trematosaurs.

In most localities where trematosaurs have been discovered, they are not associated with reptilian remains of any sort; and in both Greenland and Spitzbergen the trematosaurs are found with an abundant fish fauna and in a series of beds which are, in part at least, marine in nature. This has suggested the possibility that the trematosaurs were a group which had evolved toward a life in the seas, paralleling in a sense the plesiosaurs of later Mesozoic days just as, for example, other Triassic labyrinthodonts paralleled in fresh waters the reptilian phytosaurs and the crocodilians which replaced them. The larval amphibian cannot, in general, stand salinity in the water in which it develops; but there is no reason why a metamorphosed, air-breathing adult cannot have lived in the sea, returning to fresh water to breed — an anadromous mode of life comparable to that of the salmon. The history of actinopterygian fish life suggests (although

proof is inadequate) that there was at about the beginning of the Mesozoic a strong tendency amongst these fishes for a shift from fresh to salt waters. It is not improbable that the trematosaurs may have begun in the Permian as freshwater fish-eaters and followed their prey into the sea in the early Triassic.

If this were the course of evolution of trematosaur habits, the experiment cannot be said to have been a successful one, for the time range of the family is short. All known forms are from early Triassic deposits. The German finds of *Trematosaurus* are from the Lower Triassic — the Bunter — and the Russian *Trematosaurus* is apparently of similar age. In South Africa the trematosaur finds are likewise in Lower Triassic beds. The Indian *Gondwanosaurus* is found in beds which are definitely Lower Triassic, and the Spitzbergen and Greenland localities are so early as to be frequently termed "Eotriassic".

The one known major variation among trematosaurs has to do with skull length, as variable here as in the later plesiosaurs of presumed similar habits. The problem as to which is the primitive skull shape in the group is by no means simple. The extreme elongation seen in *Aphaneramma* is obviously not primitive, and one tends to go to the other extreme and assume that the short-skulled type of *Peltostega* or *Lyrocephalus* is the basic pattern. But this is not too satisfactory a conclusion, for the triangular shape found here is not a primitive one by any means. Possibly one of the intermediate types, such as *Trematosaurus* or *Platystega*, with a moderate degree of snout elongation, represents the central stock. From such a form a further elongation would lead to the *Tertrema-Stoschiosaurus-Gondwanosaurus-Aphaneramma* type; secondary snout reduction would lead logically to the peculiar short triangular type of *Lyrocephalus* and *Peltostega*.

The trematosaurs have been customarily grouped with other Triassic families in the "grade" Stereospondyli. But while they show marked advances in skull structure, comparable in many ways to those seen in capitosaurs, their vertebral structure, as recently described by Nilsson, is not at all stereospondylous. The vertebral type which is provisionally associated with *Lyrocephalus* is that of a typical rhachitome, differing little from that of the *Eryops* group; that of *Aphaneramma* is of similar nature, fundamentally, for while the pleurocentra are unossified generous space for cartilaginous pleurocentra is present. If vertebral structure were used as the sole diagnostic character, inclusion of the trematosaurs in the Rhachitomi

would be demanded despite their pronounced divergence in other structural features.

Although as advanced in structure as other Triassic labyrinthodonts, their anatomy shows the trematosaurs to be widely divergent from the other common families of that age, here grouped as the Stereospondyli. The metoposaurs and brachyopoids are far more progressive in their attainment of a true stereospondylous vertebral structure. Säve-Söderbergh (1935, p. 91) would bracket the trematosaurs with the metoposaurs in a common suborder, but it is difficult to imagine any two groups more divergent in almost every repsect. The only similarity is the fact that some (but not all) trematosaurs are elongate post-orbitally as are the metoposaurs. The "advanced" basicranial structure of the trematosaurs, with an extremely long pterygoid contact and the construction of a sub-occipital parasphenoidal "shelf", is quite different from that seen in other Triassic groups — even the capitosaurs, from which the divergence in vertebral structure is not as great.

One possible line of ancestry of the trematosaurs is that advocated by Efremov and Bystrow (Efremov 1940, p. 94; Bystrow and Efremov 1940, p. 143). They point out that *Thoösuchus* (here termed *Volgasaurus*), a member of the benthosuchid group of neorhachitomes, is fairly similar to *Trematosaurus* in its skull proportions. It is possible that there is a genetic relationship here, and that the trematosaurs arose from neorhachitomes of the late Permian. However, there is a considerable gap to jump in palatal construction; the actual topography of the *Thoösuchus* skull is not particularly close to that of the trematosaurs; and *Thoösuchus* seems on the whole to be close to the line leading to the capitosaurs.

It has long been recognized that *Archegosaurus* and the trematosaurs were similar in general proportions as well as in probable mode of life, and it has been considered as a possibility that the trematosaurs are descended from this older type of piscivorous temnospondyls. Säve-Söderbergh, although advocating, as noted, a distant trematosaur-metoposaur relationship, was inclined to consider *Archegosaurus* as still more closely related. The fact that the trematosaurs are persistently rhachitomous tends to close the gap to a degree. In palatal construction, certain of the archegosaur features are rather similar to those of the trematosaurs. There is, however, a radically different situation as regards palate-braincase articulation. In *Archegosaurus* there persists the ancient, essentially Carboniferous, condition of a movable joint between braincase and palate; in trematosaurs, we find here an extremely broad fusion of parasphenoid and pterygoid.

Platyops of the Russian Permian, as we have noted, tends to bridge the gap. It would appear, on current evidence, that we have here a parasphenoid-pterygoid fusion formed independently of that in the "normal" line of neorhachitomes. In them, apparently, a firm union was first established at the position of the primitive basipterygoid articulation, and then gradually expanded antero-posteriorly. In *Platyops*, it would seem, there was a broad apposition of parasphenoid and pterygoid so that when fusion occurred, it was from the first elongate antero-posteriorly in typical trematosaur fashion. It is possible that we have in *Archegosaurus-Platyops-Trematosaurus* a morphological series which may be close to a true evolutionary "phylum".

We must note, however, that even *Archegosaurus* is rather more elongate pre-orbitally than many trematosaurs, and *Platyops* is extremely long-snouted. Efremov, indeed, suggests that *Aphaneramma* is a *Platyops* descendant, while *Trematosaurus* has been derived from the neorhachitomes — a thesis which implies that the trematosaurs are not a natural assemblage. This, however, seems to be contradicted by numerous common structural features seen in long-snouted and short-snouted members of the group. It is, of course, possible that there has been a marked reversal of evolutionary trends, and that the short-snouted members of the Trematosauridae have become secondarily abbreviated from the *Platyops* condition. It is, however, reasonable to suggest that *Platyops* may be to a degree off the direct line, and that the trematosaurs' line of ascent lay through more modestly developed forms of the type of *Melosaurus*.

It thus appears probable that the trematosaurs have evolved from the typical rhachitomes by an evolutionary line independent of that leading to the typical stereospondyls. They cannot, therefore, be included in the Stereospondyli, if that group be retained with any claim to being a natural assemblage. One solution would be to retain them within the Rhachitomi. But apart from vertebral structure, they have so little in common with the earlier members of that group as to make a definition of the Rhachitomi almost impossible if they are included. We propose here to consider that the trematosaurs form a separate Suborder Trematosauria, paralleling in time and many structural features the Suborder Stereospondyli, in which latter group we here include the remaining advanced temnospondyls. A proper vertical classification would include the archegosaurids among the Trematosauria as presumed ancestors. However, in the present state of uncertainty as to the phyletic sequence, it seems better to retain these forms, in "horizontal" fashion, among the Rhachitomi.

NEORHACHITOMES

The temnospondyls remaining for consideration include a variety of forms from the Triassic to which the term Stereospondyli is customarily applied, and a number of types from the later Permian and early Triassic which are transitional in nature, currently termed "neorhachitomes". This entire assemblage is here included in the Suborder Stereospondyli in a modified use of that term. In the present section are discussed: (1) the more primitive neorhachitomes, grouped in the Superfamily Rhinesuchoidea, and including the genera *Rhinesuchus, Rhinesuchoides Uranocentrodon, Laccocephalus, Lydekkerina, Broomulus, Putterillia, Sclerothorax* and ? *Borcosaurus*; and (2) more advanced neorhachitomes classed with the Triassic capitosaurs in the Capitosauroidea and including *Benthosuchus, Wetlugasaurus, Volgasaurus, Volgasuchus, Sassenisaurus, Gondwanosaurus, Pachygonia,* and ?"*Bothriceps*" *major.*

Rhinesuchus

(Fig. 36)

The geologically earliest form definitely assignable to the neorhachitomes and perhaps the most primitive structurally of the group is *Rhinesuchus* of the Middle and Upper Permian of the Beaufort beds of South Africa. Unfortunately many structural features of *Rhinesuchus* are unknown (due in great measure to the usually refractory nature of the matrix of the Middle Permian beds), but additional data are available in related genera, such as *Uranocentrodon.*

Various species have been described; the earlier taxonomic history is summarized by Haughton (1925, pp. 227–231). "*Eryops*" *africanus* of Lydekker, based on a jaw ramus from an unknown Karroo locality (?*Cisticephalus* zone) was the first of described remains; Haughton (1915, p. 77) assigned to *R. africanus* a skull and jaw from the *Cisticephalus* zone, but later retracted this. *R. whaitsi,* the genotype, was described by Broom on the basis of fragments from the *Tapinocephalus* zone; Haughton (1915, pp. 67–70, fig. 7; pl. 12, figs. 3, 4; 1925, pp. 228–230, figs. 2, 3) assigned to this species a skull from the *Endothiodon* zone and a second *Tapinocephalus* zone fragment. *R. capensis* (Haughton 1925, p. 231, figs. 3, 4) is a relatively narrow skull from the *Endothiodon* zone; *R. broomianus* (Huene 1931, pp. 160–162, fig. 1) a broad skull from the same horizon; *R. avenanti* and *R. beaufortensis,* skulls from the *Tapinocephalus* and *Endothiodon*

zones recently described (in brief) by Boonstra (1940); *R. nyasaensis* (Haughton 1927, p. 69, figs. 1, 2), a jaw from an Upper Permian horizon in Nyasaland; and Haughton (1932, p. 635) noted the presence of labyrinthodonts (unnamed) in a bonebed of the same age in the Ruhuhu region of East Africa. Whether the type of *"Eryops" africanus* is actually a *Rhinesuchus* is uncertain. *Uranocentrodon* [*Myriodon*] *senekalensis* is often included in this genus but is here considered as a separate although related form. European materials included at one time or another in *Rhinesuchus* are merely Permian remains with a generalized rhachitomous structure.

As seen from above, the skull shape is very similar to that of the eryopsids; parabolic in outline, with a rounded muzzle, and moderately developed otic notches; the jaws are rather shorter than in eryopsids, so that the jaw condyles are but little posterior to the level of the occiput; the eyes are well to the back of the midline. The skull is, further, much more depressed than in *Eryops* and its close relatives. The sutures of the skull roof have never been described; since, however, those seen in close relatives of *Rhinesuchus*, such as *Uranocentrodon*, are similar to those of eryopsids, it is reasonable to assume a pattern of the same type here.

The palate (Watson 1919, pp. 10–12, fig. 3; Haughton 1925, figs. 2, 4) is comparable in many regards to that of *Eryops* but shows modifications and advances diagnostic of the neorhachitomes — although certain of these advances have already been seen in various eryopsoid and even edopsoid genera. The palatal vacuities are considerably larger than in *Eryops* and have (so to speak) eaten away the anterior end of the pterygoid, so that this bone has lost contact with the vomer. Significant also is the broadening and flattening of the parasphenoid-pterygoid contact in the position of the once movable basal articulation; the body of the parasphenoid, once rounded beneath the basisphenoid area, is now considerably flattened. In *Rhinesuchus* and in the other late Permian and Triassic genera considered in this and later sections, no arterial grooves or foramina are visible on the surface of the parasphenoid. It seems reasonable to believe that as a result of parasphenoidal expansion, the carotid artery and its palatine branch enter the parasphenoid beneath the cover of its postero-lateral margin and run forward in the substance of the bone (cf. *Benthosuchus*). As in a number of rhachitomes (although not in the more primitive genera) and in later stereospondyls in general, there has been an increase in the number of palatal teeth. A transverse row unites the vomerine fangs; another row runs pos-

teriorly past the choana; a third row begins at the palatine tusk-pair and extends the length of the palatine and ectopterygoid. Much of the remainder of the palate was denticulate. The marginal teeth are small and numerous. Small anterior palatine fenestrae, sometimes confluent, received the tips of mandibular tusks.

Instead of a tripartite condyle or paired condyles closely apposed as seen in eryopsoids, there are in *Rhinesuchus* two distinct and well separated exoccipital condyles, although a much reduced basioccipital may unite them ventrally. The exoccipitals reach upward to the occipital flanges of the postparietals but leave an unossified supraoccipital area. A considerably increased development of occipital flanges of postparietal and tabular is characteristic of *Rhinesuchus* and other neorhachitomes. The tabular flange turns medially far downward along the course of the paroccipital bar, but in *Rhinesuchus,* in contrast to various more advanced neorhachitomes, the endochondral ossification of the bar (opisthotic bone) is still visible posteriorly. A hypoglossal foramen persisted. Of more internal structures, almost nothing is known except for the presence of an epipterygoid which, as ossified, apparently consisted of little but the columella cranii. Little is known of the postcranial skeleton except the presence of typical rhachitomous intercentra.

Uranocentrodon

(Figs. 2, 13, 36)

Excellently preserved and nearly complete skeletons of a large amphibian from the *Lystrosaurus* zone (basal Triassic) of Senekal, Orange Free State, were described by Hoepen (1911) as "*Myriodon*" *senekalensis*. Almost simultaneously Broom (1912) described the same form as *Rhinesuchus major*. *Myriodon* being preoccupied, it was replaced by *Uranocentrodon* (Hoepen 1915, 1917; Haughton 1915, pp. 70–76, pl. 12; figs. 1, 2; Broom 1930, pp. 1–5, figs. 1–5). The genus is apparently close to *Rhinesuchus* (Haughton 1925, p. 230), but is distinctly more advanced in structure.

The skull roof pattern is closely comparable to that of the eryopsids in every regard (if allowance be made for facial elongation). The shape is similar to that of *Rhinesuchus,* but the facial region is rather more developed and the orbits are closer together. The palate likewise appears to be very similar to that of *Rhinesuchus,* despite certain supposed differences. A shagreen of small teeth covered much of the vomer, pterygoid and parasphenoid.

The occiput was depressed — more so, apparently, than in *Rhinesuchus* — but the basioccipital, on the other hand, was better developed. A seemingly significant feature in strong contrast with *Rhinesuchus* is the absence of the opisthotic from the paroccipital bar.

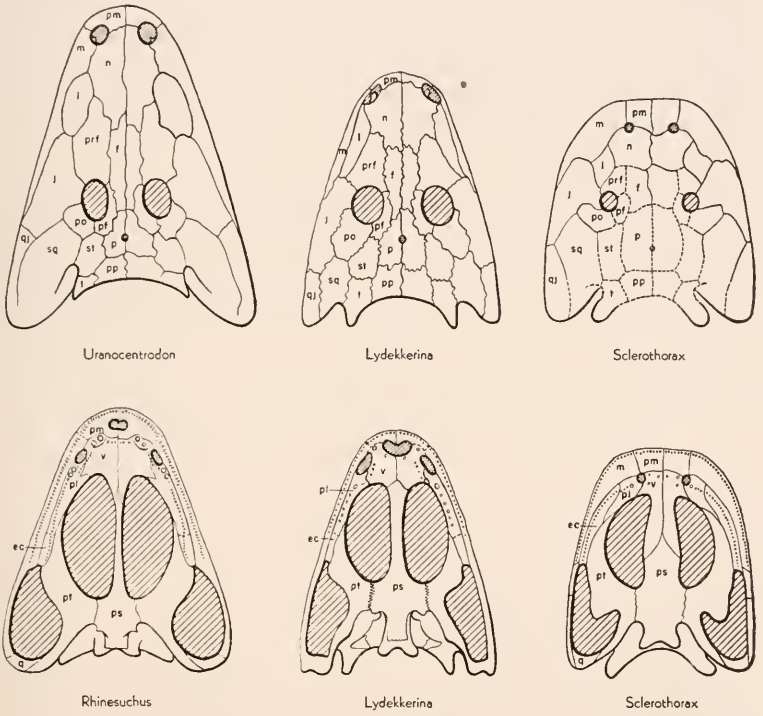

Fig. 36. Neorhachitomes. *Uranocentrodon* mainly after Broom; *Rhinesuchus* after Broom; *Lydekkerina* after Watson, Broili and Schroeder; *Sclerothorax* after Huene.

The jaws are quite comparable to the eryopsid pattern; the coronoids are toothed and there is a pair of tusks, larger than usual, on the anterior end of the dentary. There are remains of the branchial arch skeleton, showing three arches.

The slabs on which the remains are preserved show nearly complete postcranial skeletons, including articulated limbs and an *Eryops*-like armor. The vertebral column includes typical rhachitomous inter-

centra, and rather well developed pleurocentra. The body was rather more elongate than in *Eryops*; there were 29 presacral vertebrae. The articulated limb elements appear to have been built on an *Eryops*-like pattern, but are much less robust than in that genus. The postcranial skeleton as a whole confirms the impression gained from the skull that these South African neorhachitomes were to some extent reverting to a more completely aquatic existence. The ilium is described as having a shaft directed posteriorly rather than in the vertical position common in rhachitomes. Some ossified carpal and tarsal elements are preserved, and feet with phalangeal formulae of 2.3.3.3. and 2.2.3.4.3.

Probably generically identical with *U. senekalensis* is *"Laccosaurus" watsoni* (Haughton 1925, pp. 230, 234–236, figs. 5–7). This species was founded on a nearly complete skull from the *Cisticephalus* zone of the late Permian of the Karroo, a horizon just below that in which *U. senekalensis* occurs. As noted below, *Laccocephalus* appears to be similar to *Uranocentrodon* except for the absence of palatal denticles; *"Laccosaurus"* is said to be very similar to *Laccocephalus* except for the presence of such denticles, leaving little grounds for generic separation. Haughton's description of the skull roof (not figured) applies precisely to that of *Uranocentrodon*. Except for features easily attributable to differences in nature of preservation, Haughton's account of the posterior part of the palate and of the occiput agree well with *Uranocentrodon*. Very possibly the boundary between *Endothiodon* and *Cisticephalus* zones in the Upper Permian marks the change from *Rhinesuchus* to *Uranocentrodon* stages in this evolutionary series of neorhachitomes.

Piveteau (1926, p. 55, pl. 1, figs. 1–4) has described, from the Lower Triassic of Madagascar, a lower jaw, presumably of a neorhachitome, which he compares with *Uranocentrodon*; the generic and specific relationship is uncertain.

Laccocephalus

Described by Watson (1919, pp. 18–20, fig. 10, pl. 2), the only known remains of *L. insperatus* consist of an incomplete skull from the Smithfield district of the Orange Free State, and probably from the basal Triassic *Lystrosaurus* zone. The skull outlines, as restored, are similar to those of the contemporary *Uranocentrodon*, except for a slightly slimmer muzzle. The palate, with the exception noted

above, appears to be similar to the palate of that genus. As in *Uranocentrodon*, and in contrast with *Rhinesuchus*, the opisthotic does not appear on the paroccipital process. The specimen is mainly of interest in showing on fractured surfaces various internal structural details including ossified basisphenoid, basioccipital and epipterygoid and a small prootic. Particularly significant is the region of the basal articulation, shown in Watson's plate 2, figure A. As can be seen, the structure here is essentially that seen in *Eryops*. In a natural section, an unossified area is found in a recess on the medial aspect of the conjoined pterygoid and epipterygoid. This was undoubtedly filled in life by a basipterygoid process of the basisphenoid, exactly comparable to that present in ossified form in *Eryops*. This construction, it may be emphasized, differs from that in the more advanced capitosauroids, in which the epipterygoid has withdrawn from the socket for the basipterygoid process. A retention of epipterygoid participation is, however, seen in Triassic metoposaurs and trematosaurs.

The structures found in this genus are essentially those to be expected in *Uranocentrodon*; in fact there is little to distinguish the two genera except that Haughton (1925, pp. 231–233) notes the absence here of palatal denticles, present in *Uranocentrodon*.

Lydekkerina

(Figs. 13, 36)

L. huxleyi has been successively described by Broom (1915, pp. 366–368, fig. 3; cf. also 1930, pp. 5–7), Watson (1912, pp. 584–585, fig. 6; 1919, pp. 12–18, figs. 4–9), and by Broili and Schroeder (1937a, pp. 39–54). Nearly the complete anatomy is known of this rather small neorhachitome from the *Lystrosaurus* zone of South Africa. The skull contours are of the generalized rhachitome type, but the face is rather short, with the orbits not far back of the middle of the skull length. The pattern of the roofing bones is that of normal rhachitomes, but the lacrimal is elongate, reaching the naris, and the prefrontal extends far ventrally, restricting the anterior development of the jugal. The lateral line grooves take the unusual form of discontinuous pits.

The general stage of development of the palatal structures and the parasphenoid is that seen in *Rhinesuchus* and *Uranocentrodon*. The cultriform process is broad. In occipital aspect the skull is, again,

similar to those two genera; as in the former, but not the latter, the opisthotic is present in the paroccipital bar. There appears to be a basioccipital. The exoccipital has begun the forward growth and invasion of the otic area which becomes intensified in later genera. The more anterior regions of the braincase are unknown. The jaw is of normal structure.

In the postcranial skeleton, there has been recognized a weak ventral armor. The vertebrae are rhachitomous but the pleurocentra are only feebly developed. The dermal shoulder girdle was considerably expanded and flattened ventrally. In the type material the posterior projection of the interclavicle was relatively short and broadly rounded; in material from another locality, Broom notes greater elongation to a pointed termination, suggesting lack of specific identity. The pubis was unossified. The limb bones are rather short and poorly ossified, but as far as seen are of an eryopsid type.

In its relatively short face, *Lydekkerina* is in contrast with most of the South African neorhachitomes and is suggestive of the initiation of brachyopoid conditions.

Broomulus gen. nov.

(Fig. 25)

This genus is here erected for *"Lydekkerina" dutoiti* (Broom 1930, pp. 9–10, fig. 9) from the *Lystrosaurus* zone at Harrismith, O.F.S. The skull roof is of a normal rhachitomous pattern but differs notably from other neorhachitomes in the marked shortening of the face, combined with unusual skull breadth, features which may be considered as diagnostic of the genus. Skull breadth and length are approximately equal. The pre-orbital section of the skull scarcely exceeds the post-orbital in length; perhaps in relation to this, the lacrimals enter the narial boundary. The orbits are relatively close together, so that the frontal appears to enter (barely) the orbital margin, whereas the jugals, on the other hand, are broadly expanded below the orbits. As figured by Broom, the postorbital meets the parietal and separates postfrontal and supratemporal. This unusual condition is present in *Dvinosaurus* (and ichthyostegals). *Broomulus*, however, shows no apparent similarities to *Dvinosaurus* in other regards, and the pattern here may be worthy of re-examination.

It is possible that this skull roof is generically identical with the very badly preserved skull which is the type of *Putterillia platyceps*

(Broom 1930, pp. 8–9, figs. 7, 9a). Little can be made of the upper surface except the fact that the skull proportions were similar to those of *Broomulus*, from the same locality in the *Lystrosaurus* zone. An associated dermal shoulder girdle (Fig. 13) differs markedly from that of any other *Lystrosaurus* zone form in the broad, short interclavicle and long apposition of clavicular margins. The palate is little better preserved than the skull roof, but shows indications of a neorhachitomous pattern in some respects. There appears, however, to have been a "stereospondylous" condition in an apparent suture between exoccipital and pterygoid. As in the case of *Lydekkerina*, there are here suggestions of a brachyopoid trend.

Rhinesuchoides

The single described skull and jaws of *R. tenuiceps* is from the *Tapinocephalus* zone of the Karroo (Olson and Broom 1937, pp. 617–619, figs. 6, 7). The general structure, as far as can be determined, is similar to that of the contemporary *Rhinesuchus*. However, the skull is elongated in the pre-orbital region, so that the length is nearly twice the width; the muzzle is, however, broadly rounded. No sutures are discernible on the skull roof and nothing is known of the palate or braincase.

The genus is of interest in showing the initiation of skull shape variability at an early stage of the evolution of the neorhachitomes, and is suggestive of ancestry or parallelism to the long-snouted neorhachitomes of the Eotriassic — particularly *Wetlugasaurus*. In default of any further data, however, it is difficult to place this form.

Sclerothorax

(Fig. 36)

Apparently *S. hypselonotus* (Huene 1932) is an aberrant neorhachitome surviving in the Middle Bunter (Lower Triassic) of Germany. The material, from Queck in Oberhessen, consists of two partial skeletons, one including the skull. The animal was of modest size, the skull length being but 18 cm., the trunk length some 45–50 cm.

The skull, as described by Huene, is of a peculiar type — very short and broad, with small centrally situated orbits, tiny external

nares placed far in from the margins of the snout, and prominent otic notches bounded posteriorly by lateral expansions of the tabulars. Because of the nature of the material the skull roof sutures are difficult to determine, but the pattern seems to be a modification of the normal one in rhachitomes.

On the palatal surface the internal nares (like the external ones) are small and situated far forward and centrally; in correlation with this is a changed deployment of the palatal elements in this region. The vomers are described as comprising much of the region usually occupied by the cultriform process of the parasphenoid. The remainder of this central bar, included in the parasphenoid, is very broad and flat. The vomerine dentition appears to consist of a few teeth; the palatine and ectopterygoid bear the customary neorhachitomous tooth rows. The palatal vacuities are of moderate size and the pterygoids extend well forward toward (but not to) the vomers. In contrast to the anterior region, the posterior portion of the palatal aspect compares closely with such a neorhachitome as *Lydekkerina*.

Between the two specimens, most of the postcranial skeleton is known. The general impression is that of a typical rhachitome not far removed from the eryopsid type, with no indication of body depression. There is little limb material, but the girdles are fairly well preserved. The interclavicle was greatly expanded; the pubis still ossified. In the vertebral column the high-spined neural arches are reminiscent of the eryopsids, but the central structure shows definite advances. The posterior trunk vertebrae and caudals are still typically rhachitomous, with pleurocentra definitely present in one specimen, but the intercentra are much enlarged. In the more anterior vertebrae there are gaps remaining for small pleurocentra (presumably present in cartilage) but the intercentra, although only superficially ossified, reach upward broadly to the neural arch and may have been converted into complete rings.

Even if it be noted that poor preservation renders certain of the described features of *Sclerothorax* doubtful, the genus is a puzzling one. The postcranial skeleton is on the whole apparently rather primitive except for the progressive development in the vertebral centra. The skull, however, is advanced in structure, greatly shortened and strangely modified anteriorly. There is, nevertheless, no reason to believe that the genus is at all closely related to the short-headed stereospondylous forms described later. *Sclerothorax* is best interpreted as representing a late sterile side-branch of the neorhachitomes of the later Permian.

Boreosaurus

We may briefly note here *B. thorslundi*, recently described by Nilsson (1943, pp. 34–41, figs. 21–25, pl. 9), from the "Eotriassic" of Spitzbergen. The only material consists, all too inadequately, of natural casts of the meckelian cavity of the jaw, from which few distinctive characters can be determined except the presence of a well-developed retroarticular process. The jaw is markedly curved, indicating a short-headed condition, comparable to that found in *Dvinosaurus* and the brachyopoids, and Nilsson suggests possible reference to one or the other of these types. Geography suggests to that author relationship to *Dvinosaurus*, chronology suggests the brachyopids. However, *Sclerothorax* of Huene is an essentially contemporaneous animal of similar skull contours, and not too far removed geographically to be suggested as a related type; the lydekkerinids of South Africa are not dissimilar in proportions.

Benthosuchus

(Figs. 2, 5–8, 10, 12, 13, 37)

With this genus we begin a discussion of a series of long-faced neorhachitomes which are suggestive of ancestry to the Triassic capitosaurs and which are mainly from the "Eotriassic" of Russia. *Benthosuchus* is selected for initial discussion because it is very thoroughly described by Bystrow and Efremov (1940). Because of our incomplete knowledge of other neorhachitomes, a relatively full account of the structures seemingly characteristic of this genus is given here.

The genotypic species was first described as *Benthosaurus sushkini* (Efremov 1929); the generic name proving to be preoccupied, it was replaced by *Benthosuchus*. *Rasaurus* (Kusmin 1938), based on fragmentary materials from zone V of northern Russia, appears to be similar if not identical. There are a number of skulls and large series of disarticulated postcranial materials from the "Eotriassic" Zone V of the Sharjenga River region of the Timan district of northeastern European Russia.

The skull materials include growth stages which show progressive elongation of the snout. Skull lengths range from 27.5 mm. up to a maximum of 80 cm.; *Benthosuchus* as an adult was a large amphibian.

The skull shape is essentially an elongate triangle, with a narrow but somewhat blunted snout, the external nares close to the tip.

The length of the snout anterior to the orbits is about twice the post-orbital skull length. Otic notches are well developed, and the tabulars are rather conspicuously expanded into postero-laterally developed lappets. The skull is moderately depressed, the width being on the order of three times the height.

There are well developed lateral line grooves, with a transverse commissure on the snout, typical lyrae in the supra-orbital grooves and a pronounced Z-shaped curve in the lacrimal region of the infra-orbital — a pattern repeated in the capitosaurs. The arrangement of the dermal skull elements is that of a very normal rhachitomous type and needs no detailed description. The elements between orbit and naris are, of course, elongate; the lacrimal, although long, reaches neither orbit nor naris; the orbits are not widely separated but the pre- and postfrontals retain contact above the orbital rim. The skull table pattern is normal; postparietals are well developed; the supra-temporal fails to enter the margin of the otic notch.

The *Benthosuchus* skull pattern could be readily derived from that of such a form as *Uranocentrodon* (or the eryopsids) with little change except for facial elongation, and such a young skull as that in Bystrow and Efremov's figure 25 (1940) is very similar in all features to *Uranocentrodon*.

In palatal view, there are interpterygoid vacuities of considerable size, although their lateral expansion is limited by the relatively narrow snout. The pterygoids do not reach farther forward than the posterior ends of the palatines. There is a broad contact of parasphenoid and pterygoid — broader than in the South African genera — but the exoccipital does not enter into a suture with the pterygoids, as it does in the typical stereospondyls. There are confluent anterior palatine foramina for lower jaw tusks. The palatal teeth are developed in the fashion seen in a few earlier and nearly all later labyrinthodonts. A line of small teeth extends medially from the vomerine tusks, but, in relation to the constriction of the rostrum, curves backward in pendant fashion toward the midline. A second row of teeth, medial to the choana, extends backward to the palatine tusk region; from these latter structures, a long line of teeth extends back along palatine and ectopterygoid. The high quadrate ramus of the pterygoid has as in primitive rhachitomes a deep "tympanic excavation". The epipterygoid is represented by a stout columella, which did not touch the braincase. Very probably, as restored by Bystrow and Efremov (1940, fig. 34), a cartilaginous extension may have reached the quadrate, but presumably otic and columellar

processes did not join dorsally. The restoration of the palato-quadrate cartilage in their figures 33 etc., in which it is shown as extending forward to fuse with the nasal capsule is, of course, hypothetical.

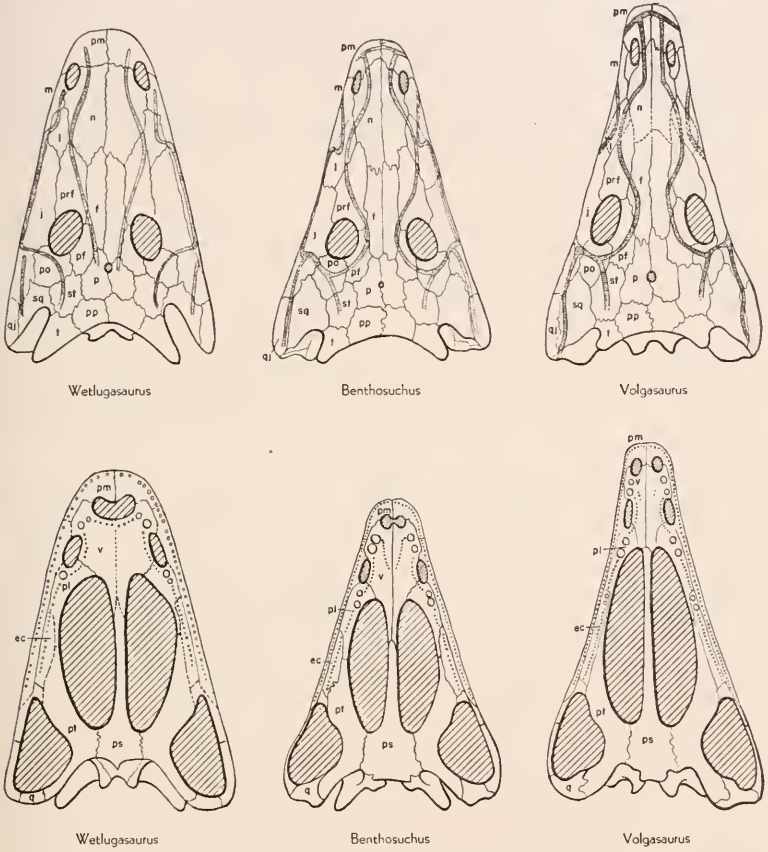

Fig. 37. Russian neorhachitomes. After Bystrow and Efremov.

The epipterygoid does not enter into the region of the basal articulation; this is entirely carried by the pterygoid, in which a deep "conical recess" (Fig. 6; Bystrow and Efremov, figs. 10, 12, 18) sheathed the cartilaginous basipterygoid process of the basisphenoid. This specialized exclusion of the epipterygoid from the basal articulation is repeated in the capitosaurs, but not in metoposaurs or trematosaurs.

The long cultriform process of the parasphenoid extends forward dorsally to the region of the anterior palatine fenestrae, but ventrally it is concealed for much of its length by posterior processes of the vomers. The cultriform process is somewhat flattened; the body of the parasphenoid is somewhat more expanded posteriorly than in the South African genera. A pronounced ridge (the crista parapterygoidea of Bystrow and Efremov) runs diagonally backward and outward on the dorsal surface to extend the parasphenoid-pterygoid suture upward behind the "conical recess"; a similar construction was present in *Eryops*.

The course of the internal carotid seen here appears to be typical of most stereospondyls (Bystrow and Efremov, fig. 10). It enters the parasphenoid posterolaterally, and courses forward through the bone. Internally the carotid gives off a palatine artery which emerges above the parasphenoid into the posterior margin of the interpterygoid vacuity. The carotid proper emerges dorsally and runs forward in a groove between parasphenoid and the cartilaginous basisphenoid to the point where it presumably turned upward, in normal fashion, into the braincase.

In the braincase proper, only three ossified elements are known — an expanded exoccipital, a vestigial prootic and a sphenethmoid. Basioccipital and supraoccipital areas were cartilaginous. The distinctly paired condyles are borne on the greatly developed exoccipitals. These elements send inward the usual flanges beneath the medullary region, and also mediodorsal flanges partially roofing the endocranial cavity. Dorsally they meet the descending flanges of the postparietals. Lateral to the posttemporal fenestra, the exoccipital meets a descending flange of the tabular mid-way of the paroccipital process, the two elements jointly substituting for the absent opisthotics. The exoccipitals extend far forward along the lateral walls of the braincase, having apparently taken over essentially the area of the absent opisthotic and completely surrounding the vagus foramen. No hypoglossal foramen is identified; openings in this region are described as nutrient in nature. An antero-ventral prolongation of the exoccipital has a broad sutural union with the parasphenoid. Above this there is a funnel-shaped lateral expansion enclosing a "tympanic recess" (Bystrow and Efremov, figs. 11, 12) obviously associated with the fenestra ovalis. There is, in a large specimen, a vestigial prootic, but no ossified opisthotic nor basisphenoid. A sphenethmoid of modest dimensions is comparable to the central portion of the sphenethmoid present in primitive rhachitomes. The

stapes is of essentially the same pattern as that of *Edops* or *Eryops*.

The jaw is slender, but with a typical arrangement of elements. The posterior coronoid bears a row of teeth; there is a prominent pair of tusks near the symphysis. There is a single meckelian fenestra and a prominent retroarticular process. In addition to the main lateral line groove of the jaw (sulcus dentalis), there is a ventrally directed groove (sulcus marginalis) and a short dorsal spur running forward on the surangular (sulcus accessorius).

In contrast to most other neorhachitomes, *Benthosuchus* is represented by a large amount of postcranial material; this is, unfortunately, not articulated. In the vertebral column there are neural arches with a low but stout spine and prominent transverse processes. Intercentra are of the rhachitomous type but reach far dorsally. Pleurocentra were not discovered. It is obvious, however, from the shape of the intercentra that they must have been present, and of fairly good size, as cartilaginous structures, for there are gaps remaining for them between successive intercentra. The cervical ribs are distinctly double-headed; the dorsal ribs, as in typical rhachitomes, are broad-headed but without ossified evidence of distinction between capitulum and tuberculum. Uncinate processes are variably developed. There was a large sacral rib apparently comparable to that of *Eryops*.

The dermal shoulder girdle presents a broad, flattened ventral surface with both clavicles and interclavicle expanded and sculptured. The interclavicle is broadly rounded posteriorly; anteriorly it narrows between the clavicles, which approach one another closely at its tip. The ascending process of the clavicle and the "stem" of a characteristic capping type of cleithrum are both short, indicating body flattening. The primary girdle is represented by a single ossification, scapular in nature, since the area preserved includes the general region of the supraglenoid buttress and the base of the scapular blade. In the small pelvic girdle, ilium and ischium have been discovered, but the pubis was presumably cartilaginous. The iliac blade was low and irregularly expanded dorsally. The limbs were small and, at the best, incompletely ossified; obviously terrestrial locomotion was limited. In a number of features the major limb elements are closely comparable to those of the Eryopsidae.

The basal structural features seen in *Benthosuchus* are in general agreement with those of other neorhachitomes, as far as they are known, and lead us to believe that various other points of internal and postcranial anatomy seen in the present genus may well have

been features of neorhachitomes in general. A consideration of these features strengthens the belief that the neorhachitomes were derived from *Eryops*-like amphibians of the earlier Permian, and represent stages in degeneration toward the flat-bodied, weakly-ossified water-dwelling "stereospondyls" of the Triassic.

The generic specializations of *Benthosuchus* lie for the most part in the elongation of the skull and in associated modifications of skull roof and palate. These specializations are definitely suggestive, as noted by Efremov and Bystrow, of the capitosaur type. Säve-Söderbergh (1937, pp. 203–204) believed *Benthosuchus* to be particularly close to *Mastodonsaurus*, but as Bystrow and Efremov point out (1940, p. 141) the resemblances are not particularly great.

Wetlugasaurus

(Fig. 37)

W. angustifrons was described by Riabinin in 1930, from materials collected from the Eotriassic of the Vetluga River in southern Timan, USSR; these materials included several skulls, with a maximum length of 160 mm., and a variety of postcranial elements. *"Capitosaurus" volgensis* of Hartmann-Weinberg and Kusmin (1936), from deposits of the same zone on the middle Volga was recognized by its describers to be closely related to if not identical with *Wetlugasaurus*, and Efremov has described an additional specimen from that region (1940, pp. 97–98, pl. 1).

Very similar, if not identical amphibians appear to have been widespread. Säve-Söderbergh (1935, pp. 122–131, fig. 53, pls. 1, 2) has described *W. groenlandicus* from the Eotriassic of East Greenland; the sole specimen is the posterior end of a skull roof. Watson (1942, pp. 81–82) notes undescribed *Lystrosaurus* zone material from South Africa which may be *Wetlugasaurus*, and a skull intermediate between *Rhinesuchus* and *Wetlugasaurus* in Parrington's collections from an approximately equivalent zone in East Africa. *"Lydekkerina" putterilli* (Broom 1930, p. 7, fig. 6) from the *Lystrosaurus* zone may be a form of the sort noted by Watson. This consists only of the posterior part of a dermal skull roof which tapers markedly anteriorly, with orbits relatively close together, suggesting an elongate and narrow snout.

The skull of *Wetlugasaurus* (cf. Bystrow and Efremov 1940) is on the whole very similar to that of *Benthosuchus*, but somewhat more

primitive and closer to the rhinesuchid type. Pre-orbital elongation is not as pronounced; the muzzle is broader and more rounded. Apparently in relation to this last, the transverse row of vomerine teeth forms nearly a straight line. The anterior palatal vacuities are broadly confluent. Tabular "horns" are more pronounced than in *Benthosuchus*. The skull is somewhat less depressed than in *Benthosuchus*, the parasphenoid slightly narrower, endochondral ossification apparently somewhat less reduced. Associated limb elements were poorly ossified; in the vertebral column, pleurocentra were present but were strongly reduced.

Wetlugasaurus appears to bridge much of the gap between *Benthosuchus* and the rhinesuchoids in skull shape and other features.

Volgasaurus

(Fig. 37)

V. kalajevi was founded by Kusmin (1937) on the posterior part of a skull from zone V of the middle Volga region, and was thought by its describer to be a trematosaurid. The photographs illustrating this specimen are none too clear, but as far as can be seen, this skull is very similar to if not identical with *Thoösuchus*, described subsequently by Efremov (1940, pp. 93–97, figs. 1–5) with "*Lyrocephalus*" *acutirostris* Hartmann-Weinberg and Kusmin (1936a) as the genotype. To the same generic group, *fide* Efremov, belong "*Trematosuchus*" *jakovlevi* Riabinin (1926) and "*T.*" *weidenbaumi* Kusmin (1935). All are from Zone V of the Kineshma region of the Volga. As redescribed by Efremov, *Volgasaurus* [*Thoösuchus*] is a neorhachitomous form rather than a trematosaurid. It shows general similarities to *Benthosuchus* of the same age. However the skull is more elongate; the anterior palatal vacuities are discrete; large tusks are present in the ectopterygoid tooth row. These features suggested to Efremov that "*Thoösuchus*" represents the beginning of trematosaur-like specializations, but there is no concrete evidence that the resemblances denote actual relationship rather than a parallelism shown in similar skull shape and due to associated predaceous habits.

Volgasuchus

Represented only by the posterior half of a small skull (Efremov 1940, p. 98, figs. 8, 9) from the "Eotriassic" Zone V of the Kineshma region of the Volga, *V. cornutus* shows pronounced sculptured tabular

"horns", but in other regards appears to be very similar to *Wetlugasaurus*.

Sassenisaurus

Wiman (1915, pp. 22–23, pl. 9) described as *Cyclotosaurus*? *spitzbergensis* the anterior end of the palate of a large labyrinthodont from the early Triassic of Spitzbergen. This has been restudied by Nilsson (1942), who points out that it is not a *Cyclotosaurus* nor, apparently, a capitosaurid of any sort, but represents a new benthosuchid genus. It differs, however, from *Benthosuchus* and *Wetlugasaurus* in the broad choanae, the relatively narrow cultriform process and in the single, heart-shaped anterior palatal vacuity. Nilsson (1943, pp. 23–34, figs. 13–20, pls. 4, 6–8) has described jaw specimens reasonably assigned to this form; the data agree with the general structure noted for the benthosuchid jaw.

Gondwanosaurus

Apparently similar to the Russian neorhachitomes was *G. bijorensis* (Lydekker 1885) from Bijori village in the Central Provinces of India, in deposits which are currently regarded as belonging to the uppermost part of the Damuda series of the Upper Permian or earliest Triassic. The sole specimen of *G. bijorensis* includes the cast of a head, some 30 cm. in length, from which nearly all the bone is gone. The general proportions are those of the Russian neorhachitomes, such as *Wetlugasaurus*, or the capitosaurs. The face is rather elongate, tapering to a rounded snout; the eyes are well back of the center of the skull length, and there are very prominent tabular "horns". The orbits are proportionally somewhat larger than in most neorhachitomes (or capitosaurs). The palatal vacuities are large; the parasphenoid-pterygoid contact is as elongate as in capitosaurs. Unfortunately the choanae, the area of the anterior palatal vacuities, and the palatal dentition are not known.

Part of the postcranial skeleton is present. As far as seen the dermal shoulder girdle is capitosaur-like. Vertebrae are adequately represented by impressions. These are definitely rhachitomous in nature, for there are large spaces for unossified pleurocentra, as in many neorhachitomes, even though the vertebrae are from the front part of the column — in which region capitosaurs tend to be advanced. Hence *Gondwanosaurus* is best classified among the neorhachitomes, although apparently close to the capitosaurs.

Pachygonia

The type of *P. incurvata* is the posterior part of a jaw from the early Triassic Panchet deposits of India (Huxley 1865, pp. 6–8, figs. 1, 2). The jaw is not in itself definitive but the general proportions, sculpture and arrangement of the lateral line grooves are closely comparable to those of the benthosuchids, and it is not improbable that the genus belongs here. Other fragments assigned to this genus by Lydekker on various occasions are doubtful. *"Goniogliptus" huxleyi* (Lydekker 1882, pp. 26–27, pl. 1, figs. 5, 8) does not belong to that slender-jawed trematosaur genus and is quite similar to *Pachygonia*. We have noted the presence of the presumed benthosuchid *Gondwanosaurus* in the Bijori beds, of nearly the same age.

"Bothriceps" major

The oldest amphibian known from Australia is the type of this species (Woodward 1909). This comes from the Airly mine near Lithgow, N.S.W., in the Upper Permian Newcastle Coal Measures. The specimen consists of the skull and much of the skeleton of an amphibian seen in dorsal view in a slab of oil shale. The general impression is that of a partially grown form; little can be made of the structure of the vertebrae or of such limb bones as are preserved. The skull is 15 cm. in length; sutures are not visible. The shape is in general that of the benthosuchids, the skull moderately elongate and slender-snouted, and with the orbits at about the mid-point of the length; on the assumption that the individual is somewhat immature, a rather more elongate adult may be deduced. The general appearance and geologic age suggest that the form is a neorhachitome, but there is, of course, no real proof of the fact. There is no reason to associate this animal with the short-faced brachyopid *Bothriceps*; but it seems inadvisable to found a new genus on this poorly-known specimen.

DISCUSSION

Consideration of the various genera of the later Permian and "Eotriassic" reviewed in this section indicates that the concept of a "neorhachitomous" grade of evolution among the rhachitomes is a useful one. We recognize that it is difficult to clearly demarcate

the older and more primitive neorhachitomes from the ancestral eryopsoids, and almost impossible to separate the advanced benthosuchids from the capitosaurs, next to be discussed. Nevertheless, the members of the neorhachitomous assemblage characteristically exhibit a long series of significant features. These include: flattening of the skull; retention or, more probably, reappearance in the adult of lateral line grooves; primitive presence of a normal eryopsid skull pattern, but variation in facial (not post-orbital) length; palatal vacuities large, the pterygoids typically reaching only to the posterior end of the palatines; rows of palatal teeth rather than single tusk-pairs on the lateral series of palatal elements; parasphenoid somewhat expanded in its cultriform process and considerably expanded and flattened posteriorly; a broad contact of parasphenoid with pterygoid, and eventually with exoccipital as well; braincase elements, except exoccipitals, unossified or feeby developed; paired exoccipital condyles; the opisthotic reduced and seldom appearing in the paroccipital process, being replaced by a descending flange of the tabular; jaw articulation moved forward to a position about on the level of the occiput; vertebrae rhachitomous but pleurocentra reduced or unossified; dermal shoulder girdle expanded and flattened ventrally; pubis cartilaginous; limbs small and poorly ossified. Almost all of these features are associated with a degenerative trend toward a water-dwelling existence. Of these features, some were attained, apparently in parallel fashion, by certain of the earlier rhachitomes; many were retained with little change among the Triassic stereospondyls.

One might with considerable justification unite the neorhachitomes in a single group. The problem, however, is none too simple. For one thing, the capitosaurs are certainly descended from the benthosuchids, and any separation of the two is obviously artificial. We might, then, expand the neorhachitomes to include the capitosaurs, and, indeed, Bystrow and Efremov (1940, p. 143) have suggested that the entire series from *Rhinesuchus* to the capitosaurs might be included in a single comprehensive family. However, a more analytical treatment is, we think, preferable. The benthosuchids appear to be specifically pre-capitosaurs; the members of the African assemblage, are not only rather more primitive but also seem to be potentially ancestral to other stereospondyls as well. We therefore suggest a classification of a different sort, in which the more primitive or generalized neorhachitomes be included in a Superfamily Rhinesuchoidea, while the benthosuchids be united with their capitosaur descendants

in the Superfamily Capitosauroidea. Superficially the two may be distinguished by the retention in most rhinesuchoids of the general eryopsid skull shape, in contrast to the elongated snout of the capitosauroids. A more significant difference appears to lie in the construction of the region of the basal articulation. In benthosuchids and in their capitosaurid descendants the basipterygoid process was received in a "conical recess" formed by the pterygoid alone. This appears to be a distinctive specialization. In primitive rhachitomes the epipterygoid shared in the formation of the socket for this process, and the same condition persisted, among typical Triassic temnospondyls, in the metoposaurs and trematosaurs. Among the "African" neorhachitomes, this region is known only in *Laccocephalus*; here the usual condition prevailed, and it is reasonable to assume that it was diagnostic for the Rhinesuchoidea in general.

Of the rhinesuchoids, Watson united the African genera *Rhinesuchus, Uranocentrodon* and *Laccocephalus* in the family Rhinesuchidae. All have "normal" eryopsid skull shapes, and seem to be similar in most features. However *Rhinesuchus* seems to be definitely more primitive in the retention of the opisthotic in the paroccipital bar (seemingly a significant feature); the placing of the other two genera in a separate family, Uranocentrodontidae, seems appropriate on the basis of our present knowledge. *Rhinesuchus* is definitely earlier in age as well as apparently more primitive. *Rhinesuchoides,* poorly known, may, at a guess, be bracketed with *Rhinesuchus* merely on the basis of age. *Lydekkerina* was made the type of a separate family, the Lydekkerinidae, by Watson mainly on the basis of the shortened face, and *Broomulus* may be included here. *Sclerothorax* presumably is a specialized survivor which must be placed in a separate family; possibly *Boreosaurus* may belong here.

Despite the parallelisms which certainly occurred in various cases among the rhachitomes in general, there is no reason to believe that the rhinesuchoids are not a monophyletic assemblage derived from the eryopsids or closely allied forms. Further, they form a group from which it is possible that many if not all of the Triassic stereospondyl families may have been derived. The capitosauroids have, as far as known, changed in few features apart from facial elongation and modification of the basicranial region. Derivation from them of metoposaurs or brachyopids is reasonable, although there is little positive proof. It is not impossible that the trematosaurs, too, are descended from the rhinesuchoids, but here, as has been seen, another line of descent is probable.

The remaining genera are: *Wetlugasaurus, Benthosuchus, Volgasuchus* and *Volgasaurus* — all characteristic of the Russian Eotriassic — *Sassenisaurus* of Spitzbergen, *Pachygonia* and *Gondwanosaurus* of India and *"Bothriceps" major* of Australia. These may be reasonably included in the Benthosuchidae. They appear to be certainly ancestral to the Capitosauridae (discussed below) and may be, with these descendants, placed in the Capitosauroidea. There is little to suggest that they are in any way closely related to the ancestry of other Triassic labyrinthodonts.

We have noted earlier the general problem of division of the temnospondyls. There is at no point any sharp break in the main evolutionary series from primitive rhachitomes on upward to the advanced Triassic types characteristic of the advanced stereospondylous condition. It is, however, convenient to separate upper and lower portions of the series, and establish a group of Stereospondyli to include the more advanced forms. Of the typical Triassic groups concerned, the capitosaurs are readily derivable from and closely connected with the benthosuchid neorhachitomes, and hence these latter should be included in the stereospondylous assemblage. Further, if the short-skulled brachyopoids and metoposaurs (discussed later) be included in the Stereospondyli, the common ancestors of these forms and the capitosaurs should be included in the group, if it is to be a "natural" one. Such common ancestors must be as low as the rhinesuchoid level. In consequence, the Stereospondyli, as here modified, include the neorhachitomes as well as the capitosaurs and brachyopoids (including metoposaurs), while excluding the trematosaurs (which developed advanced characters, it would seem, in parallel fashion.). The fact that the neorhachitomes are not technically stereospondylous in vertebral structure need not be of concern; in reality this structure is almost entirely confined to the brachyopoid group. The gap between the rhinesuchids at the base of the stereospondyls as here defined and the *Eryops* group is small, but, as in any phyletic line which is fairly well known, any point of cleavage must be an arbitrary one.

CAPITOSAURS

The Triassic capitosaurs are obviously little modified descendants of the long-snouted neorhachitomes of the Eotriassic and are here placed with them in the Capitosauroidea. In earlier times most were included in two genera, *Capitosaurus* and *Mastodonsaurus*; but in

better accord with current taxonomic practices a number of other genera — *Parotosaurus, Cyclotosaurus, Stenotosaurus, Stanocephalosaurus* and (?) *Kestrosaurus* — may be recognized.

Capitosaurus

(Fig. 38)

The type species of *Capitosaurus* is *C. arenaceus*, of which the only known specimen is an imperfect skull, about 30 cm. long, from the Lower Keuper of Benk in upper Franconia. The species was first described over a century ago, and more recently discussed by Broili (1915). Despite its imperfections — including absence of the posterior margin, and the fact that the skull roof is represented only by impressions of the inner surface — the specimen demonstrated a distinctive organization which differs markedly from other common Triassic forms. The skull is considerably elongated anterior to the orbits so that these openings appear well to the back. The general roof pattern is that of the more generalized rhachitomes; pattern and skull shape are both fairly similar to and could be derived from conditions seen in the Russian neorhachitomes such as *Wetlugasaurus*. There are, however, certain differences. The nares are somewhat smaller and more anteriorly placed. The orbits, which in this and most capitosaurids are small and situated rather medially, are bounded in part by the frontals, with a separation of pre- and postfrontal elements. The postorbital has its center of ossification far down the side of the cheek and tends to crowd the jugal out of its position along the orbital rim (*Wetlugasaurus* shows an initial stage in this development). Although the posterior margin of the skull is missing, we can be sure (from conditions in related types) that the tabulars were at least prominently extended as superficial "horns" as in the benthosuchids. Except for the few differences noted above, the capitosaurid skull roof can be superposed almost perfectly on that of such a neorhachitome as *Wetlugasaurus*. The palate is imperfect, and is not figured here, but as far as it can be determined it appears to have been of the type seen in other capitosaurs and described below.

This capitosaurid type of skull, once recognized in this species, was later identified in a considerable amount of Triassic material, and *Capitosaurus* became a prominent and seemingly widespread genus. In more recent decades, however, it has become increasingly

apparent that under this generic term had been described a number of distinct, although closely related, genera. It has long been recognized, for example, that the typical capitosaur of the Upper Trias of Europe is one in which the tabulars have united posteriorly to enclose the otic notch. Fraas, in 1889 (p. 121), proposed the term *Cyclotosaurus* to cover such forms, assuming that the less specialized ancestral types, common in the Lower Triassic, could remain in *Capitosaurus*. This procedure has been generally followed. But, in fact, we do not know this region in the type species of *Capitosaurus*, just described. As a series of authors — Schroeder, Broili, Watson, etc. — have pointed out, this type is Upper Triassic and hence probably identical with *Cyclotosaurus* rather than an open-notched type. What to do taxonomically is a difficult problem. We propose here to steer a safe course in the matter, and suggest that, since *Capitosaurus* is essentially indeterminate, the use of the term be restricted to the type, and that more readily definable generic terms be used for the adequately known forms — *Parotosaurus*, for example, for the typical early Triassic "*Capitosaurus*" with open otic notch, *Cyclotosaurus* for the well known closed-notch type of the European Upper Trias.

Parotosaurus

(Figs. 2, 10, 38, 39)

Capitosaurus is generally regarded as being most typically represented by "*Capitosaurus*" *nasutus*, a relatively primitive form, with open otic notches, from the Middle Bunter of Bernburg. As noted above, the generic identity is more than questionable. Because of this situation, Jaekel in 1922 (p. 8) coined the term *Parotosaurus*, which we shall here use for *P. nasutus* and capitosaurs which are, or are thought to be, related.

P. nasutus is known from an abundance of skull material, with lengths generally of 25–35 cm., described by Meyer (1858, pp. 222–229, pls. 24–26, 28), Jaekel (1922, pl. 1 etc.), Schroeder (1913, pls. 17, 19–21) and Roepke (1923) amongst others. The general skull pattern is of the sort described for the *Capitosaurus* type; as in that form the snout is moderately rounded. The otic notch is open; the postorbitals are produced laterally; the postfrontals are crowded posteriorly much more than in the *Capitosaurus* type or in *Cyclotosaurus*.

As has been said, it was long common to assign to "*Capitosaurus*" almost all remains of capitosaurid type, with the implication that

they were generically identical with the form here called *Parotosaurus nasutus*. It has, however, been increasingly realized that various genera were concerned in this complex. Certain forms obviously differing from *nasutus* have been accorded generic separation, as *Cyclotosaurus* and *Stanocephalosaurus*, and in a following section another distinct variant is recognized generically as *Stenotosaurus*. There still remains, however, a considerable series of material from the Lower Triassic which has never been removed from "*Capitosaurus*" — i.e., *Parotosaurus*. Some may belong to that genus, but some of the forms concerned may well prove to be distinct. This material may be reviewed at this point.

A number of specimens from the Lower and Middle Triassic of Europe have been referred to as "*Capitosaurus*" in the sense of the present genus. Of these the best preserved is "*C.*" *helgolandiae*. This is represented by a nearly complete skull from Helgoland. It has been figured by Schroeder (1913; cf. Jaekel 1922, pp. 15–17, pl. 1) but, since very few sutures are indicated, it is not figured here. The skull was found in deposits of Bunter type which are assumed, although on little but lithological grounds, to be of early Triassic age — possibly very early in the Bunter. The skull is one of large size for this time — some 46 cm. in length, as compared with much smaller average figures for *P. nasutus*. The facial region is much more slender than in that species, the skull of a more pointed triangular shape, the tabular "horns" more slender. Few sutures are visible. The postorbital extends, as in *P. nasutus*, far lateral to the orbit. On the other hand, the position of the center of ossification of the postfrontal suggests that this element extended well forward above the orbit, giving the frontal but little room on the orbital margin — a feature found in "*Cyclotosaurus*" *albertyni* and *Stanocephalosaurus*. The palate is that of a typical capitosaur, except that the parasphenoid-pterygoid suture is relatively short, and the cultriform process rather narrow for a capitosaur as opposed to a neorhachitome. The structure in general suggests that despite its large size this form was a relatively primitive member of the group. It may be generically identical with *P. nasutus*, but more detailed knowledge is needed.

"*Capitosaurus*" *fronto* of Meyer (1858, pp. 229–236, pl. 28, fig. 2) is known only from a posterior half of a skull roof found in the Bernburg Bunter with *P. nasutus*, but certainly distinct from it. This is indicated by the fact that although the roofing pattern is capitosaurid, the sculpture is different, lateral line grooves are absent, the orbits

smaller and more lateral in position, the otic notch more widely open, the skull as a whole probably relatively broader and shorter in the facial region — differences which are certainly not entirely associated with age (although the skull is smaller).

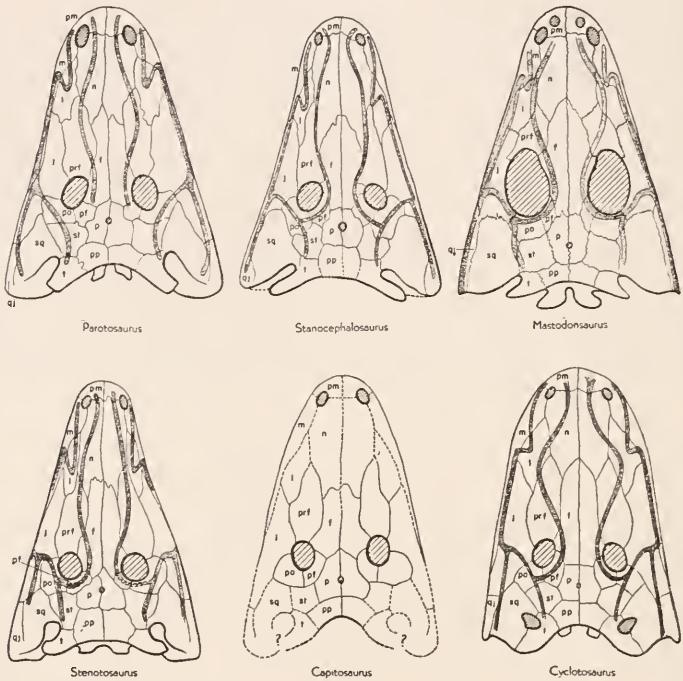

Fig. 38. Capitosaurid skull roofs. *Parotosaurus* mainly after Schroeder; *Mastodonsaurus* composite, mainly after Fraas; *Stenotosaurus*, reconstructed from Swinton's data; *Capitosaurus* after Broili; *Cyclotosaurus* mainly after Huene.

"Capitosaurus" polaris of Wiman (1915, pp. 21–22, pl. 8) is an incomplete skull roof of capitosaur type from Spitzbergen; in the development of its postorbital it is very similar to *P. nasutus*.

"Capitosaurus" silesiacus (Kunisch 1890) is a fragment of a capitosaur skull roof from the Lower Wellenkalk — early Middle Triassic — of Silesia, which, as far as preserved, is very similar to *P. nasutus*. Perhaps to be associated is a single intercentrum, thin antero-

posteriorly but expanded dorsally so as to form a kidney-shaped structure partially enclosing the notochord in proto-stereospondylous fashion.

Corroy (1928, pp. 109–110, pl. 2) has cited several species of *"Cyclotosaurus"* from the Wellenkalk (Lower Muschelkalk) of Lor-

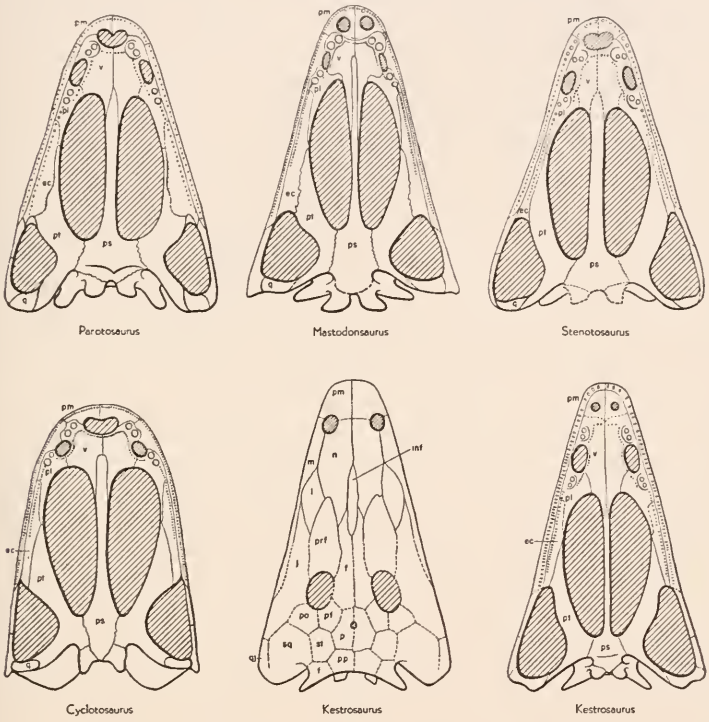

Fig. 39. Capitosaurid palates and *Kestrosaurus*. *Parotosaurus*, *Cyclotosaurus*, *Mastodonsaurus*, composite; *Stenotosaurus* after Meyer, Swinton; *Kestrosaurus*, restored after Haughton.

raine; the material is capitosaurid, but fragmentary and apparently generically indeterminate.

"Mastodonsaurus" weigelti (Wagner 1935) from Bernburg is, as far as can be made out from its describer's photographs, identical in all regards with *P. nasutus* from this same locality (cf. Nilsson 1943a, p. 253); this similarity is particularly marked in the complete

skull figured by Wagner which is herewith designated as the holotype of the species.

"*Capitosaurus*" remains from the typical Lower Triassic of Russia ("Zone VI" of Efremov) were first described by Sushkin (1927) in a morphological description of internal structures of two skulls found at Mount Great Bogdo in the region north of the Caspian. Efremov (1932) reported further scraps from this region; "*Capitosaurus*" *bogdoanus* was associated, as at Bernburg, with *Trematosaurus brauni*, strongly suggesting that the material pertains to *P. nasutus* or a closely related form. *Capitosaurus* is also reported, with doubt, from the same zone near Čkalov (Orenburg) by Efremov.

A number of specimens ascribed to "*Capitosaurus*" or "*Cyclotosaurus*" have been described from the *Cynognathus* zone of South Africa; the horizon appears to be equivalent to the typical Lower Triassic of Europe and hence these forms may pertain, in part, at least, to *Parotosaurus*. Broom (1909, p. 271) early described, in brief fashion, an incomplete and rather small skull as "*Capitosaurus*" *africanus*; Watson in 1919 (pp. 22–29, figs. 12–16) gave an interesting account of internal structures in a second skull of rather good size which he referred to this genus but gave no specific name. Haughton in 1925 (pp. 239–241, figs. 8–10) described and figured a third specimen, nearly complete but badly weathered dorsally, which he assigned to Broom's species; he notes that the internal structures agree well with Watson's descriptions except for a lesser degree of ossification. A fourth specimen is that of Broili and Schroeder (1937b); this is, like Watson's specimen, of large size (with an estimated length of 75–80 cm.) but appeared to its describers to be sufficiently different to merit a new specific name as "*Capitosaurus*" *haughtoni*. Although very fragmentary, the specimen shows various interesting structural features. And finally, we may note that Broom (1904) early described an incomplete skull of a capitosaur of large size (probably 65–70 cm. long) as "*Cyclotosaurus*" *albertyni*. The reference to this Upper Triassic genus is highly improbable, and may well have been based on size, since he notes that the otic notch region is not complete although he believes it to have been of a closed type. Broom suggests that the large teeth given the generic names *Syphonodon* and *Ptychosphenodon* by Seeley (1907, 1908) may belong to this form. This African material is of considerable morphological interest, but from a systematic point of view merely demonstrates the widespread occurrence of the capitosaurs in that large and small representatives of the family were present in South Africa in early Triassic times.

A primitive capitosaur, presumably of the *Parotosaurus* type, is said to occur in the Beacon Hill shale of the Lower Triassic Hawkesbury series of New South Wales, Australia (Watson in David 1932, p. 76). Presumably to this genus is to be assigned a "*Mastodonsaurus*" dermal plate reported by Stephens (1886, 1887b) from the Hawkesbury beds of the Sydney region (Cockatoo Island).

Welles (1946) reports numerous specimens of "*Capitosaurus*" from the Moenkopi of Arizona.

We may note some of the morphological features of early Triassic capitosaurs, gleaned from this varied material here grouped under *Parotosaurus* and from the material of the several closely related genera that follow. The skull roof pattern and contours were, as noted for the *Capitosaurus* type, almost identical with those of *Wetlugasaurus* and other long-snouted neorhachitomes of the Eotriassic of Russia. Within *Parotosaurus* and the related genera noted below, there are diagnostic features in the variable development of the tabulars, the presence or absence of closed otic openings, and variations in the development of postfrontal and postorbital etc. as well as in the greater or lesser development of a pointed snout. In general, however, the pattern is a consistently uniform one.

The palatal structure, too, is very uniform in these forms; further, it is very similar in most respects to that of the neorhachitomes of the *Wetlugasaurus* group. The two types are almost identical in the degree of development of the interpterygoid vacuities; the anterior palatal vacuity; the position of the choanae; most features of the dentition; the general pattern of the palatal elements and of the basicranial region. The jaw articulation of early capitosaurs is, on the average, more anterior in position than in the Russian neorhachitomes, although the difference is slight; the length of the sutural union between parasphenoid and pterygoid is somewhat greater, and the line of suture is not a direct antero-posterior one as in the benthosuchids, but tilts laterally at its posterior end; the transverse tooth lines on the vomers connect the two tusk-pairs directly rather than having the V-shaped arrangement seen in the typical benthosuchids.

Evidence of the nature of deeper structures has been slowly accumulating since the time of Quenstedt (1850). Of contributions by recent authors we may note accounts by Watson (1919, pp. 22–29, figs. 11–16), based on a specifically unidentified "*Capitosaurus*" from South Africa; Roepke (1923) on *Parotosaurus nasutus*; Sushkin (1927, figs. 3, 4, 15 etc.) who gives braincase data on a capitosaur from the Russian Lower Triassic; Haughton (1925, pp. 238–248, figs. 8–14)

on *Kestrosaurus* and *"Capitosaurus" africanus*; Broili and Schroeder (1937b) on an African form.

As seen in posterior view, the occiput is similar in all essential features to that of the neorhachitomes, although the depth is apparently slightly less. The braincase is very incompletely ossified, although discrete ossifications, considerably reduced, representing sphenethmoid, basisphenoid, prootic and basioccipital, may be present in specimens which are relatively large or presumably mature; as in the neorhachitomes, the exoccipitals, with very distinctly paired condyles, are strongly ossified and, invading the otic region (with opisthotic reduction), have a powerful articulation with the parasphenoid and also articulate with the dorsal surface of the pterygoid; this union is not visible superficially. The epipterygoid is much expanded. In *Kestrosaurus*, the pterygoid has, as in the neorhachitomes, a large socket for the unossified basipterygoid process and the same "conical recess" is present in *Cyclotosaurus* (Quenstedt 1850, pl. 2, *k'*). In general the structures are of a sort which are readily derivable and little changed from those of the Russian neorhachitomes.

The lower jaw structure is poorly known, but appears to have been similar to that of benthosuchids (cf. Nilsson 1943, 1944; Edinger 1937, etc.). The general proportions are similar in the two cases. Both have: a well developed pair of tusks near the symphysis; well developed lateral line grooves including, at least in some capitosaurs, the accessory sulcus seen in *Benthosuchus* etc.; a well developed retroarticular process; a posterior meckelian fenestra but no evidence of an anterior one; a prearticular which terminated anteriorly at a transverse suture with the middle coronoid.

In contrast with the considerable number of skull finds is the fact that very little postcranial material has been reported. There are practically no definitely associated limb or girdle structures. In several cases vertebral intercentra of a rhachitomous or sub-stereospondylous nature have been reported as possibly associated. Such association is reasonable but the evidence is poor.

Cyclotosaurus

(Figs. 13, 38, 39)

This generic term was coined by Fraas (1889) for application to the characteristic Upper Triassic European capitosaur with closed

otic notches, *C. robustus*, first described by Meyer and Plieninger (1844, pl. 9 etc.) and later by Quenstedt (1850), Meyer (1855, pls. 59, 61, 64) and Fraas (1889, pp. 121–136, pls. 9–11) among others. The material is from the "Schilfsandstein" of the Middle Keuper of the Stuttgart district. This is a rather large amphibian, with a skull length of 50–70 cm. The facial portion of the skull is elongated in capitosaur fashion, but the whole skull is broad and the snout broadly rounded. The roofing pattern is that of a typical capitosaur, with one notable exception characteristic of the genus: the tabular is broadly expanded postero-laterally to enclose completely the otic notch and, with the equally expanded squamosal, to form a broad shelf of bone extending back far beyond the normal posterior limits of the skull. It will also be noted that the postorbital is not as prominent as in *Parotosaurus*.

Like the roof, the palate is, in most respects, quite similar to that of other capitosaurs. The basicranial region, however, is of a very "advanced" type, for (as clearly seen in Quenstedt's specimen) the exoccipitals meet the pterygoid broadly in ventral view. In this the genus has paralleled the contemporary brachyopoids and departs from more primitive capitosaurid conditions. The situation suggests a general "drift" in this direction among late Triassic stereospondyls. Part of the internal structure is visible in Quenstedt's clear and seemingly accurate figures and shows features generally comparable with those of neorhachitomes.

Little is known of the postcranial skeleton except for expanded dermal shoulder plates and a few vertebrae. These last are of an advanced type. Intercentra from the posterior part of the trunk are still incomplete rings. But in the anterior part of the body we find the true "stereospondylous" condition. These structures are now complete discs, with a notochordal pit close to the top margin. However they are very thin antero-posteriorly, and somewhat wedge-shaped, thinner at the top. Even in these vertebrae, however, space still remains for small cartilaginous pleurocentra. They suggest that the body was a very short one, although there was presumably much cartilage between successive intercentra.

In various respects, particularly in the basicranial region, *Cyclotosaurus* is comparable to the metoposaurs. The resemblances are obviously due to parallelism; but this parallelism is suggestive of a real (if distant) relationship of capitosaurs and metoposaurs due to their common descent from neorhachitomes of the late Permian and earliest Trias.

Various other materials from the upper part of the Trias, and hence essentially contemporaneous, appear to belong to *Cyclotosaurus* or to be at least closely related.

Kuhn (1932, pp. 100–112, pl. 3) has figured as *C. ebrachensis* a fine skull, similar to *C. robustus*, except for smaller size (35 cm.); this is from the Blasensandstein, also in the Middle Keuper but at a somewhat higher level. From the Stubensandstein at the top of the true Keuper, a much higher level, have come two large incomplete skulls, with estimated lengths of 48 and 60 cm. These specimens (from Pfaffenhofen in Württemberg), have been described by Fraas (1913, pp. 288–294, pls. 18–22) as *Cyclotosaurus postumus* and *C. mordax*. Both are capitosaurs and do not belong to *Mastodonsaurus*, hence in size and stratigraphic position may well belong to *Cyclotosaurus*. But in neither case is the otic region preserved, and it is possible that one or both pertain to some parallel development within the family. Fraas further suggests in this connection that fragments, practically indeterminate in nature, from a still higher level, the Rhaetic, of Schotmar, Prussia, are *Cyclotosaurus*; there is no proof of generic or even familial identity here.

Jaekel (1914, pp. 210–213, figs. 31–33) has described, from the uppermost (Rhaetic) beds of the Halberstadt fossil deposit, intercentra which likewise indicate the persistence into this horizon of some member of this group — possibly *Cyclotosaurus*, as the best known, at least, of late survivors. Vertebrae presumably from the anterior part of the trunk are stereospondylous — complete discs, although the notochordal perforation is well toward the top. Those probably more posterior in position are incomplete, with a V-shaped dorsal gap. Both types are somewhat narrower at the top, suggesting that small cartilaginous pleurocentra may have persisted. Because of the presence with these vertebrae of teeth with keeled tips, Jaekel erected for them a new genus, *Hercynosaurus*. However, teeth of this character appear to be not uncommon among capitosaurs, and indeed, Quenstedt nearly a century ago (1850, p. 231, pl. 2, fig. 6) noted their presence in *Cyclotosaurus robustus*. Very probably Jaekel's material is that of a "straggler" of *Cyclotosaurus* in the Rhaetic. Kuhn (1939a), in a recent discussion of the Halberstadt amphibians, has erected a new genus, *Hemprichisaurus*, for a poor snout fragment, which shows nothing to distinguish it from *Cyclotosaurus*.

Rhachitomous intercentra from the Upper Triassic of Spitzbergen (Wiman 1915, p. 25, pl. 6, figs. 1–4; Nilsson 1943a, p. 263) are pre-

sumably to be attributed to *Cyclotosaurus* or a similar form.

Apart from Europe, there are no described specimens of *Cyclotosaurus* in the Upper Triassic. However there are excellent materials of *Cyclotosaurus* or a similar form from the St. Peter's quarry in the Wianamatta Series (Upper Triassic) of the Sydney (Australia) region (Watson 1918; David 1932, pp. 76–77; Longman 1941, p. 31, etc.)

In this connection we may note the description by Longman (1941) as *Australopelor wadleyi* of a jaw fragment which he believes to be that of a capitosaurid from the Marburg Series of Queensland, thought to be of early Jurassic age. There is no sure evidence of the nature of this jaw, although it might possibly be a *Cyclotosaurus*, and the evidence for the age of the beds seems none too strong. If labyrinthodont nature and Jurassic age be confirmed, this is without question the last survivor of the labyrinthodonts.

Capitosaurus arenaceus, described above, is from the Lower Keuper and generic identity with *Cyclotosaurus* may well be suspected. However, this form is rather smaller, with a more pointed snout and minor differences in skull pattern, and may belong to some parallel line. (It was noted that if generic identity should be proved, the appropriate name *Cyclotosaurus* would disappear.)

A slender skull by no means indicates absence of the closed otic notch, however. *Cyclotosaurus stantonensis* is a form from the Lower Keuper of Staffordshire, England, still smaller in size (with a skull length of 21 cm.) and with a slender snout (Woodward 1904). The single known skull reveals most of the roof, a good occiput and the anterior part of the palate. The snout is still more slender than in the *Capitosaurus* type; the skull pattern is almost identical as far as can be seen; yet the otic notches are definitely closed posteriorly. The tabular and squamosal are, however, little expanded, and the post-otic bridge is slender. This form may well be a primitive species, with *Cyclotosaurus robustus* developed from it by expansion of the skull both fore and aft; further knowledge may indicate the advisability of generic separation.

Another find from a relatively early Upper Triassic locality is *C. papilio* of Wepfer (1923a) from the boundary between Muschelkalk and Lettenkohle in northern Baden. This, however, is only an occiput.

Fragmentary remains of English Keuper amphibians, mainly of jaw materials, have been described by a series of authors — Owen, Miall, Seeley, Smith Woodward and, most recently, Wills (1916). Most are ascribed to "*Labyrinthodon*" (a synonym of *Mastodonsaurus*)

but are, as far as they are at all identifiable, capitosaurs and, from their age, probably *Cyclotosaurus* or a similar form. *"L." leptognathus* is mainly represented by small and slender jaws which are appropriate for *C. stantonensis*. *"L." pachygnathus* includes some reptilian material, but other specimens of this species, and those of *"L." lavisi* and *Diadetognathus varvicensis*, are jaw fragments of a rather large form comparable to the continental *Cyclotosaurus*. Some of the material described as *"L." jaegeri* is the same; *"L." lanarius* and *"L." ventricosus* are merely isolated teeth.

Stenotosaurus gen. nov.

(Figs. 38, 39)

Swinton in 1927 described as *Capitosaurus semiclausus* an interesting capitosaurid from the Upper Bunter of Cappel near Villingen in the Baden Schwarzwald. The skull roof is almost completely shown, and exhibits an interesting variant of the capitosaurid pattern. The snout is rather more slender than in the typical *"Capitosaurus"*. The suborbital progress of the postorbital bone seen in *Parotosaurus* has advanced to such a degree that that element has met the prefrontal ventral to the orbit and thus excluded the jugal from the orbital margin — a feature unknown in any other labyrinthodont. Posteriorly the tabular has extended so far toward the squamosal as to nearly (but not quite) complete the enclosure of the otic notch. It is thus, as Swinton notes, approaching the *"Cyclotosaurus"* condition here. But *"Cyclotosaurus"* lacks the peculiar suborbital configuration seen here and hence the otic development of the present species is merely a parallelism. I believe that the two features mentioned make this form worthy of more than specific separation from its relatives and hence propose to characterize on this basis a new genus *Stenotosaurus* with *C. semiclausus* as the type.

The palate is preserved only in small part in Swinton's specimen. However, a century ago Meyer (1855, pp. 138–139, pl. 64, fig. 16) described as *"Labyrinthodon" fürstenbergianus* the palate of a slender-snouted labyrinthodont from Herzogenweiler, a locality also in the Schwarzwald Bunter, although from a slightly lower horizon (upper part of the Middle Bunter). This is an appropriately shaped capitosaurid palate which may well be that of the present species, as noted by Edinger (1937), who described a second, fragmentary, palate of this sort from Freudenstadt, another Middle Bunter locality in the Schwarzwald. Swinton does not figure sutures in the skull roof, but

I have restored them from indications in his excellent photograph and his text. Fraas (1896, p. 7) has referred fragments from the Bunter of Calw and Nagold to "*L.*" *fürstenberganus* on purely stratigraphic and geological grounds.

Stanocephalosaurus

(Fig. 38)

S. birdi (Brown 1933) is known from a single specimen discovered near Winslow, Arizona, in beds which its describer states to be of Middle Triassic age (Moenkopi, Welles 1946). This is a relatively slim-snouted capitosaur with open otic notches, comparable in proportions to *Stenotosaurus*; in the development of the circumorbital elements the pattern resembles the *Capitosaurus* type and *Cyclotosaurus*. The palate is perfectly comparable to the usual European capitosaur type. Welles (1946) reports further cyclotosaur-like forms from the Moenkopi. It is curious that no capitosaur has ever been identified among the numerous amphibian finds in the Chinle, Dockum and other formations of the American Upper Triassic.

Kestrosaurus

(Fig. 39)

A large skull from Senekal, Orange Free State, and probably from the Eotriassic *Procolophon* zone of the Beaufort Series, was described by Haughton (1925, pp. 242–248, figs. 11–14) as *K. dreyeri*. As its describer notes, its structure is comparable to that of the Capitosauridae, but the skull is more elongate and slender than in typical members of that group and thus closer to the benthosuchids. The palate is of a characteristic capitosauroid type in almost every regard. The parasphenoid-pterygoid suture is relatively short as in the benthosuchids, and the anterior palatal vacuities are paired, as in the benthosuchid *Volgasaurus* on the one hand, and in the capitosaur *Mastodonsaurus* on the other, rather than assuming the more usual confluent situation.

Of the dorsal surface, only the anterior half is preserved and figured. The pattern is that of other capitosauroids, with the interesting exception that a slender unpaired element comparable to the interfrontal of *Eryops* is present. On the posterior half of the skull one can, as the figure indicates, readily restore a benthosuchid or capitosaurid pattern.

Haughton describes and figures various internal structures which agree well with what is known of other capitosauroids.

Kestrosaurus is here included provisionally among the capitosaurs, but is rather primitive and somewhat transitional in nature between benthosuchids and capitosaurs — a condition also suggested by its stratigraphic position.

Mastodonsaurus

(Figs. 12, 13, 38, 39)

This capitosaur-like genus is of interest both as the earliest of labyrinthodonts to receive scientific attention and as the giant of the group — one large skull having an estimated length of 125 cm., or over four feet. Abundant remains are known from the later Triassic of central Europe.

M. giganteus (the "*Labyrinthodon jaegeri*" of Owen) is known from a number of skulls and numerous postcranial remains from the Lettenkohle of the lower Upper Triassic, particularly Gailsdorf in Swabia. Descriptions were given by Jaeger and Meyer in early days; more recently by Fraas (1889, pp. 32–93, figs. 1–5, pls. 1–5, 17), Watson (1919, pp. 36–38, fig. 22) and Huene (1922, pp. 400–410, figs. 2–12). *M. acuminatus* is a term applied to somewhat smaller and more slender skulls (? perhaps younger individuals) from Hoheneck, also in the Swabian Lettenkohle (Fraas 1889, pp. 104–115, pls. 7, 8, fig. 1) and from the same formation in Thuringia (Schmidt 1931, pp. 237–258, figs. 1–5, pls. 1–3). Fraas (1889, pp. 116, pl. 8, figs. 2–6) has described as *M. keuperinus* fragmentary remains from a somewhat higher Swabian horizon, the Schilfsandstein of the Lower Keuper. There are various other reports of fragmentary remains of *Mastodonsaurus* from central Europe (for example, from the Alpine Upper Triassic, Broili 1906), but often there is little or nothing to make generic identity certain, and we may be dealing with a *Cyclotosaurus* or *Metoposaurus*. We have noted, under the former genus, various fragments of English Keuper labyrinthodonts, some of which may belong to *Mastodonsaurus*.

The typical *Mastodonsaurus* is thus from the Upper Trias. However, remains of this genus, or a closely related form, are known from earlier portions of this period. Meyer (1855, p. 78, pl. 62, fig. 5) early described as *Xestorrhytias perrini* fragmentary remains from the Lower Muschelkalk (Wellenkalk) of Luneville. Some of the material is plagiosaurid, but the type appears to be a large capitosaur, perhaps

Mastodonsaurus. Corroy (1928, p. 111) has cited the genus from the Lorraine Wellenkalk, on the basis of fragments, and it is also reported from the Crailsheim bonebed and other German Muschelkalk localities.

The Bunter, too, includes remains of the *Mastodonsaurus* type of capitosaur. Meyer (1855, pp. 136–138, pl. 59, figs. 6, 8) early described, as *M. vaslenensis*, an incomplete small skull from the Upper Bunter of Wasselnheim in Lower Alsace. Wepfer (1922; 1922a; 1923) discovered, and described as *M. cappelensis*, a large amount of material, with skulls only about 50 cm. long, from a "Leichenfeld" in an equivalent horizon across the Rhine at Kappel, Baden. This suite of specimens was further described by Pfannenstiel (1932), whose morphological results are, however, somewhat questionable. There are no appreciable differences, as far as known, between *vaslenensis* and *cappelensis*. *M. ingens* (Trusheim 1937) is a large jaw from the Bunter of Altensteig, Mainfranken.

Although the Bunter form is certainly close to and presumably ancestral to the typical *Mastodonsaurus* of the later Trias, it is possible that the earlier species might prove to differ sufficiently to merit generic separation. However, there are, as far as can be seen, no marked differences, except for the somewhat smaller size and slightly more slender contours of the Bunter skulls. Säve-Söderbergh (1935, p. 97) has erected the genus *Heptasaurus* for the Bunter animal, but the supposed generic differences are mostly of a very minor nature and are based, apparently, on a comparison of Fraas' obviously diagrammatic figure of the outer surface of the roofing elements in *M. giganteus* with Wepfer's figure, seemingly equally diagrammatic, of the inner surface of the roof in *M. cappelensis* (cf. also Nilsson 1942, p. 95). It is possible, however, that further knowledge of internal structures and postcranial elements might validate Säve-Söderbergh's genus.

The *Mastodonsaurus* skull in general has the typical capitosaurid contours and structures. It is, however, broad posteriorly, and tapers forward evenly toward the fairly narrow muzzle.[1] The tabulars project prominently but do not close over the otic notch. The orbits are oval and of relatively as well as absolutely large size — an unusual feature in a large animal. There is no trace of the lateral and ventral expansion of the postorbital seen in many other capitosaurs. A characteristic feature is the presence, in somewhat crocodilian

[1]The swollen appearance of the lateral margin of the temporal region in Fraas' restoration does not appear in the figured actual material.

fashion, of a pair of openings in the premaxillae, presumably for accommodation of the tips of the lower jaw symphysial tusks.

The palate is that of a typical capitosaurid, notable only for the large number of teeth and the fact that the anterior palatine fenestrae are paired, although set in a common depression. Unfortunately the basicranial region is imperfectly known; it appears that the contact of pterygoid and parasphenoid was longer than in typical capitosaurs. The internal structure is inadequately known; Wepfer (1923) and Pfannenstiel (1932) have given accounts of it in *M. cappelensis*, but these accounts are unsatisfactory, both as regards illustration of the material and because of incorrect bases on which their conclusions are reached (such as the assumption that the epipterygoid formed the lateral wall of the otic capsule). It is, however, of interest that one of Wepfer's figures (1923, fig. 19) shows clearly the typical socket for the basipterygoid process in the pterygoid; it is highly probable that the structure was similar to that of other capitosaurs. The jaw, as described by Fraas and by Wepfer, is in general comparable to that of other capitosaurs, but there is said to be a unique development of a large process of the prearticular arising dorsally from the medial border of the adductor fossa.[1]

A very considerable amount of postcranial material of *M. giganteus* is known and has been described by Meyer, Fraas and Huene, and commented on by Watson; Wepfer has also figured elements of *M. cappelensis*. The vertebrae of the posterior portion of the trunk are simply enlarged crescentic intercentra of the rhachitomous type, deeply excavated centrally and, in side view, narrowed above, indicating the probable presence of small cartilaginous pleurocentra. The more anterior vertebrae, however, show a stereospondylous condition in the Upper Triassic stage; progressing forward, one sees that the ossification becomes greater in extent and that the notochordal region is restricted to a perforation situated far up toward the dorsal edge, while in lateral view the anterior and posterior edges become almost pārallel, indicating that the intercentra were either very small or absent. In the Bunter type, however, Wepfer notes that the anterior vertebrae have not quite attained the stereospondylous condition; there is a slight dorsal notch for the notochord rather than a closed perforation. The caudals are, as preserved, typically rhachitomous structures.

[1]One may reasonably suspect that, despite the seeming discrepancies and absence of this process in the specimen, the large capitosaurid mandible of "*Mentosaurus*" *waltheri* Roepke (1930) from the Lower Muschelkalk near Halle is that of a *Mastodonsaurus*.

As Watson notes, the postcranial material, although relatively feebly ossified, is in many regards highly comparable with that of *Eryops* and it is on the whole still more closely comparable with that of *Benthosuchus*.

DISCUSSION

As reviewed above, the capitosaurs are seen to be, for the most part, a compact group, showing little variation. Beginning in the early Trias with *Parotosaurus* and other relatively primitive types, we appear to witness a general evolutionary trend which culminates in the large terminal forms, *Cyclotosaurus* and *Mastodonsaurus*. There are some minor variations in skull shape, position of circumorbital elements, nature of openings for symphysial tusks, and — particularly — in the development of the prominent tabular projections. There is general agreement that with the exception of *Mastodonsaurus* all may be included in a single family, the Capitosauridae.

Mastodonsaurus is frequently placed in a distinct family from the *Capitosaurus* group. There is, however, little of importance to distinguish it from members of the Capitosauridae. If, for example, one uses the lengthy diagnoses of Säve-Söderbergh (1935, pp. 80–81), one finds that the only distinctive features cited are that the more typical capitosaurs have longer skulls, smaller orbits, somewhat larger postorbitals and somewhat differently shaped tabulars. However, these are features of generic rather than familial value. *Mastodonsaurus* seems clearly to be merely another variant of the capitosaurid type which evolved via *M. cappelensis* during the course of the Triassic.

That the Capitosauridae are closely related to and descended from the benthosuchid group of neorhachitomes is obvious. In our discussion of *Parotosaurus* we have commented on the very great similarity which exists between all known skull structures of the early capitosaurs and those of the Benthosuchidae. On such grounds, Bystrow and Efremov are inclined to include benthosuchids and capitosaurs in a common family. However, the two groups do have distinctive features, even if they are not as marked as one might have at one time expected in a shift from the "Rhachitomi" to the "Stereospondyli"; and further, certain of the cranial differences — notably in the expansion of the flat basicranial region — are still more marked in the Upper Triassic genera. Family separation of the Capitosauridae from the Benthosuchidae seems advisable.

Unfortunately, the postcranial skeleton of early capitosaurs is too poorly known to render comparison profitable. Particularly unfortunate is the paucity of data on the vertebral structure of the Bunter capitosaurs. We have noted evidence indicating that the early capitosaurs may have still been in a "neorhachitomous" stage of vertebral development, in which the intercentra were crescents, not enclosing the notochord; one Middle Triassic intercentrum shows partial — but not total — enclosure of the chorda. In the two "terminal" genera, the posterior part of the column appears to have remained in a primitive condition, but the anterior vertebrae were, by definition, stereospondylous — complete intercentral discs, in which the notochordal territory was included, and in *Mastodonsaurus*, the pleurocentra were completely reduced. There were thus, it would seem, marked intra-familial evolutionary trends in vertebral evolution.

Although the evolutionary relationships of the capitosaurs and their neorhachitomous relatives seems certain, the technical question of grouping these forms into assemblages above the family level is far from clear. As we have noted in the last section, however, it seems to us preferable to unite the Capitosauridae with the Benthosuchidae in a Superfamily Capitosauroidea.

SHORT-FACED STEREOSPONDYLS

To be considered here are several families of short-faced Triassic temnospondyls. The Brachyopidae (*Bothriceps, Brachyops, Batrachosuchus, Pelorocephalus,* ?*Tungussogyrinus*) and Plagiosauridae (*Gerrothorax, Plagiosaurus, Plagiosternum* and *Plagiosuchus*) are short-skulled types. Long-headed, but equally short-faced, and apparently related to them is the Family Metoposauridae of the late Triassic, including the European *Metoposaurus*, a large array of North American finds described as *Dictyocephalus, Anaschisma, Buettneria* etc., and recently described Indian forms. All three families are here considered to constitute the Superfamily Brachyopoidea.

Bothriceps

(Fig. 40)

This genus was described by Huxley (1859, pp. 647–649, pl. 2, figs. 1, 2) on the basis of a skull, complete but with most of the bone eroded, from an unknown horizon and locality in Australia which

Lydekker believed to have been situated in the Triassic Hawkesbury beds of New South Wales. *B. australis* was refigured by Broom in 1915 (pp. 364–366, fig. 2) and discussed by Watson, who figured the palate, in 1919 (pp. 43–44; fig. 26). The form was rather small, the skull but 10 cm. long. The skull roof of *B. australis* shows the pattern typical of most rhachitomes and stereospondyls, but is quite short and broad, the breadth being approximately the same as the width. The post-orbital region is of normal dimensions, the reduction having taken place in the facial region. The orbits are small and widely separated; the external nares, on the contrary, are rather close together in the somewhat pointed snout.

An interesting feature, repeated in the short-skulled genera which follow and in metoposaurs, is the marked backward slant of the occiput, so that the double condyles on the exoccipitals are far back of the posterior margin of the skull roof. The jaw articulation is posterior to the level of the upper part of the occiput but about opposite the condyles. The central part of the palate, which alone is known, shows a parasphenoid expanded posteriorly, having a broad articulation with the pterygoid, and a rather broad cultriform process. The exoccipital runs far forward along the lateral surface of the braincase to gain a contact with the pterygoid, but the ventral exposure of this suture is narrow. A hypoglossal foramen persists; the opisthotic is not exposed posteriorly.

No other material can be definitely assigned to this form. Stephens described (1887, 1887a) as "*Platyceps*" *wilkinsonii* (the generic name is preoccupied) several skeletons of smaller size (with head lengths of 27, 65 and 72 mm.), from the underlying Narrabeen Series of New South Wales. He suggested that they were larvae of *Bothriceps* (gills are present). The skulls are relatively shorter, but this is a juvenile character. There are prominent lateral line grooves as in *Batrachosuchus* and the plagiosaurs discussed later. Clavicles and interclavicle are broadly expanded in these small specimens as in later European plagiosaurs.

Brachyops

(Fig. 40)

B. laticeps was early described by Owen (1854) from the Lower Triassic Mangali beds of Central India. As in *Bothriceps* the description rests on a single skull, about 12 cm. long, from which the roofing

elements are eroded. It has been redescribed by Broom (1915, pp. 363–364, fig. 1); as he notes, it is similar to *Bothriceps*. However the skull is much shorter in both post-orbital and (particularly) pre-orbital regions, and the jaw articulation is situated farther forward. Thought to be approximately contemporaneous with the Mangali beds are those of the Panchet group. Quite possibly the jaw described by Lydekker (1882, pp. 24–26, pl. 1, figs. 1, 2) from the Panchet and incorrectly assigned by him to *Pachygonia incurvata* belongs to *Brachyops* or a related form. The jaw is of appropriate small size, short and strongly curved, indicating a broad, narrow skull. There is a powerful symphysial tusk (cf. *Dvinosaurus!*). In the Panchet beds (Huxley 1865, pl. 6, figs. 9–10) there are complete, if thin, ring-shaped stereospondylous vertebrae, pierced centrally for the notochord. It is improbable that they belong to *Gonioglyptus longirostris* or *Pachygonia*, the only other well-defined labyrinthodont in the beds, for these genera were presumably neorhachitomous or rhachitomous in vertebral structure. They may belong to *Brachyops* or a related genus. The early development by the brachyopids of a stereospondylous vertebra is a reasonable expectation, in view of the advanced nature of the centra in late Triassic brachyopoids.

Batrachosuchus

(Figs. 3, 40)

B. browni is based on a skull from the Lower Triassic *Cynognathus* Zone of South Africa (Broom 1903). Watson in 1919 (pp. 44–47, figs. 27, 28, pl. 1) described in detail a second skull from the same beds, to which Haughton (1925, p. 257) later gave the name *B. watsoni*. As Broom recognized, this form is closely related to the last two genera, but the skull is still more reduced in the facial region and the muzzle broadly rounded rather than pointed. The skull is much larger than in those genera, the skull length being about 25 cm. and the width rather greater. This is about the size of the plagiosaurs discussed below. The dermal bones of the skull are well seen in Watson's specimen; they are heavily pitted (although not punctate) and show a pronounced development of lateral line grooves. The posterior margin of the skull is well preserved (in contrast to the specimens of *Brachyops* and *Bothriceps*) and shows that the otic notch had been nearly completely eliminated, the back margin of the skull roof being nearly straight.

Nearly all of the palate is visible. There are large interpterygoid vacuities. The condition is more advanced than in *Bothriceps* in that the exoccipital is, as in metoposaurs, in broad contact with the pterygoid. The jaw articulation, in contrast to *Bothriceps,* has moved forward to a position anterior to the level of the condyles, and in consequence the quadrate ramus of the pterygoid is a short lateral

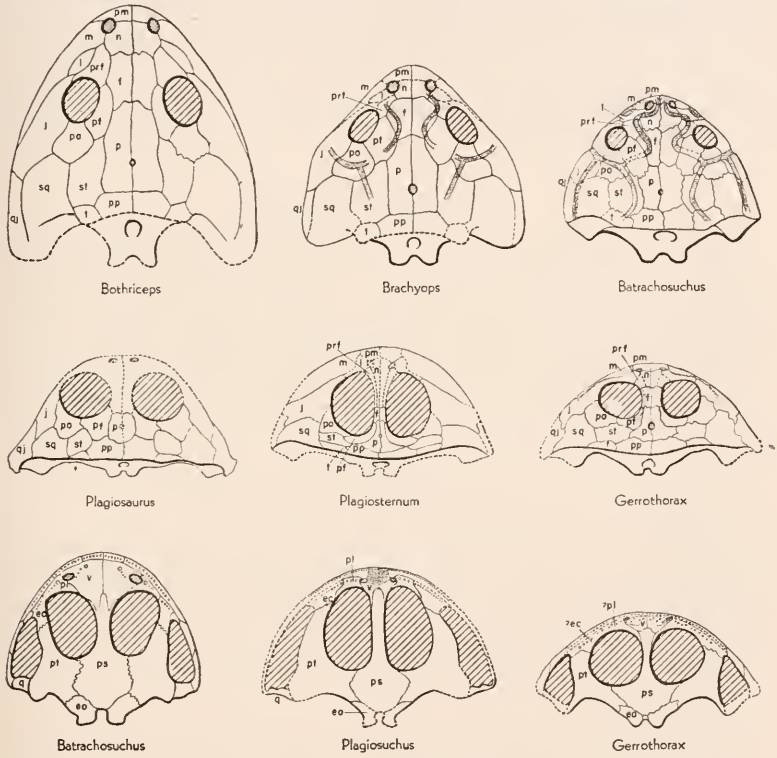

Fig. 40. Short-skulled brachyopoids. *Bothriceps, Brachyops* after Broom; *Batrachosuchus* after Watson; *Plagiosaurus* after Jaekel, Nilsson; *Plagiosternum* after Fraas, Huene, Nilsson; *Gerrothorax* after Nilsson; *Plagiosuchus* after Huene, Nilsson.

process. The back margin of this ramus of the pterygoid forms a strong descending flange. The details of the anterior part of the palate are inadequately known, although there are, however, palatal tusks on vomer and palatines, and the choanae are widely separated

(despite the fact that the external nares are close together). On the occiput neither basi- nor supraoccipital is present in the specimen described, and there is no occipital exposure of an opisthotic, the tabular extending down to a suture with the exoccipital. There is a hypoglossal foramen. There is apparently no contact between pterygoid and squamosal; the infratemporal fossa is widely open behind (cf. metoposaurs). Watson (1912, pp. 584–586, fig. 6) described an incomplete jaw; he identified but a single coronoid and a single splenial element, but otherwise the jaw shows an abbreviate modification of the typical rhachitome pattern. There was a moderately developed retroarticular process.

Pelorocephalus

The only labyrinthodont ever discovered in South America is the type of *Pelorocephalus mendozensis*, recently described by Cabrera (1944). The specimen is from the upper level of the Cacheuta beds, of Middle Triassic — possibly lowest Upper Triassic — age, in Mendoza Province, Argentina. It exhibits the palatal surface of the skull and the dorsal aspect of the lower jaws; the condition of the material is poor and little detail can be made out. There is, however, little question but that (as Cabrera notes) we are dealing with a brachyopid.

The skull proportions are similar to those of *Brachyops*; the snout is somewhat more pointed than in *Batrachosuchus*, and the interpterygoid vacuities more elongate than in that genus. As preserved, the specimen appears to show a confluent pair of anterior palatal vacuities not otherwise found in brachyopoids. Except at the posterior margin of the parasphenoid, palatal sutures are not visible. The shortening of the jaws had proceeded to the extent seen in *Batrachosuchus*. The skull length, of 245 mm., is almost exactly the same as in that genus.

Welles (1946) reports the discovery of a brachyopid in the Moenkopi of Arizona.

Tungussogyrinus

A very tiny skeleton from the Tungus basin of Siberia was described by Efremov (1939) as *T. bergi*. The deposit containing it was the Korwuntchan (Upper Angara) series, presumably of Triassic — perhaps Eotriassic — age. The specimen is obviously a larval amphibian. The skull is seen from the palatal surface; it is very short

and broad, with eyes notably far forward, jaw articulations well in advance of the condyles, and a parasphenoid very broad in both body and cultriform process. These features are, of course, immediately suggestive of the brachyopoids. However, as Efremov properly points out, they may be attributed — at least in great measure — to the fact that we are dealing with a larva. Skull and jaws may have been considerably elongated in the adult but certainly this adult would have been relatively short-faced. There were about 20 presacral vertebrae.

The vertebrae, as described by Efremov, appear diagnostic. The centra are solid, elongate structures. Efremov inclines to identify them with branchiosaur vertebrae. This identification rests, however, on the Credner restoration of such vertebrae, now known to be incorrect. Solid elongate centra are known in but one group — the plagiosaurs of the middle and later Trias, presumably of brachyopid descent. As seen above, the vertebrae of the Brachyopidae are not positively known, but may well have been of the type seen in their presumed plagiosaur descendants. Thus *Tungussogyrinus* may reasonably be classed as a brachyopoid, and, because of its presumed early Triassic age, is possibly a member of the Brachyopidae.

Gerrothorax

(Fig. 40)

This is the best known of a series of progressive (or degenerate) late Triassic short-faced types, the plagiosaurs. *Gerrothorax* was founded by Nilsson in his papers of 1934 and 1937 for the inclusion of two species, *G. rhaeticus* from the Rhaetic of Scania, and "*Plagiosaurus*" *pulcherrimus* from the Stubensandstein (Upper Keuper) of Pfaffenhofen, Württemberg. The former, first described by Nilsson, has but little of the skull, but includes much of the trunk; the latter species, originally described by Fraas (1913, pp. 282–285, pl. 16, figs. 1–3) has been rediscussed by Huene in 1922 and by Nilsson; it is represented by an excellent skull. "*Plagiosaurus*" *franconicus*, described by Kuhn (1932) on the basis of a partial interclavicle from the Middle Keuper of Ebrach, Franconia, may perhaps belong here (*fide* Nilsson), as well as "*Plagiosaurus*" *striopustulatus* (Huene 1922, pp. 439–441), based on shoulder plate fragments and vertebrae from the Keuper of Swabia.

Gerrothorax and its relatives are amphibians of rather good size, the skulls measuring on the average 26 to 30 cm. in width. The skull

in this genus and its close relatives described below is far more specialized than in the brachyopids. The sculpturing of the dermal elements of skull and shoulder is of a granular type, rather than the usual pit-and-ridge system common to labyrinthodonts. The striking feature of the skull is its excessive shortness compared to its width, with a nearly straight posterior margin and a parabolic anterior outline; the breadth in *Gerrothorax* is about 2½ times the length. As in the brachyopids described above there is a pronounced backward slant of the occiput behind the margin of the skull roof. The orbits are extremely large, leaving but a narrow bar of bone between them in the frontal region. Anterior and posterior to the orbits the normal roofing elements are present, but "stretched out" transversely to accommodate themselves to the peculiar skull shape. In *Gerrothorax* they appear, however, to have maintained their normal relations with one another despite their changed proportions. As in *Batrachosuchus* the jaw articulation lies anterior to the occiput, about on a line with the posterior margin of the roof.

The palate of *Gerrothorax* is essentially comparable to that of *Batrachosuchus*, but much shortened and broadened. Certain of the sutures between palatal elements are not clear, and there are differences in detail in the arrangement of palatal teeth, such as a tendency for tooth multiplication on the vomers. Nilsson reports that in the braincase *Gerrothorax* retained a small supraoccipital and small basioccipital and that the opisthotic is present on the posterior surface between exoccipital and tabular, whereas *Batrachosuchus* was more advanced in this regard. There is no hypoglossal foramen.

In *Gerrothorax* a considerable amount of postcranial material is known. Vertebrae are found in association with specimens of two species. The neural spines are low but stout and expanded dorsally, suggesting an intimate connection with a tough "hide" or dermal armor. The pedicel of the arch is V-shaped in lateral view, and fits into a notch between successive centra. These centra are unlike those of any other labyrinthodont group. They are reptile-like, elongate, solid structures; there is no notch or perforation for the notochord, nor are they markedly amphicoelous. Dorsally there is a groove for the neural canal, lateral to which there are slanting surfaces anteriorly and posteriorly for articulation with the two adjacent neural arches. There are articular areas on both anterior and posterior margins of the centrum for an "intercentral" attachment of the rib head; the tubercular attachment was to a low transverse process just above, on the lower edge of the neural arch. The anterior ribs, pre-

served, are distinctly double-headed, slightly expanded distally and run directly laterally, indicating that body as well as head were greatly flattened.

The dermal shoulder girdle is incompletely known, but may have resembled that of *Plagiosaurus*, described below. The Swedish material has a well preserved series of scales in chevron covering the abdomen; they correspond fairly well to those of early labyrinthodonts, and a number of associated sculptured plates indicate that the animal was also armored dorsally, with a loose carapace of ossicles. Nilsson further describes an inner series of rod-like structures which he compares to reptilian abdominal ribs.

Plagiosaurus

(Figs. 3, 12, 13, 40)

P. depressus is based on material from the Triassic deposits of Halberstadt, from an upper horizon that is currently regarded as Rhaetic in age. Originally described by Jaekel (1914, pp. 202–210, figs. 26–30), *Plagiosaurus* has been redescribed by Huene in 1922 and Nilsson in 1937 (pp. 47–48, fig. 13 etc.) and 1939. Piveteau (1928, pp. 23–29, pl. 5) ascribed to this genus vertebrae and dermal plates from the Keuper of Lunéville.

In *Plagiosaurus* the posterior portion of the skull is present, seen in dorsal view, and part of the jaw. In most regards the skull is similar to that of *Gerrothorax*, but as restored is somewhat more elongate and hence somewhat more primitive. The skull pattern shows one interesting variant in that the parietal has, so to speak, given up the struggle to maintain a contact laterally with the supratemporal, so that postfrontal and postparietal are in direct contact. The jaw is flattened dorso-ventrally, and has rather large marginal teeth as well as a pair of small symphysial fangs and further teeth on the two preserved coronoids.

Of the postcranial skeleton there is a number of associated vertebrae of the type described for *Gerrothorax*. Jaekel has given good figures of the neural arches; Piveteau has figured a number of centra. There are excellent remains of the dermal shoulder girdle; Jaekel's description has been supplemented and corrected by Nilsson (1939). The interclavicle is greatly expanded, very broad posteriorly and moderately broad, rather than pointed, anteriorly. Despite its anterior expansion, however, the broad ventral surfaces of the clavicles have a wide contact anterior to it. Unlike conditions in most

labyrinthodonts, the clavicle does not come to a point dorsally but retains a fairly broad sculptured lateral margin continuous with a low but broad cleithrum. The build of the dermal shoulder girdle proves that the body, like the skull, was much depressed; the width at the shoulder was about 4½ times the height there. A humerus of modest size, together with a partial radius, are described by Nilsson (1939); these are the only known limb elements in any plagiosaur.

Plagiosternum

(Fig. 40)

This was the first established of plagiosaur genera. The type materials of *P. granulosum*, first described by Fraas (1889, pp. 94–100, pl. 6, pl. 17, fig. 9; 1896, pp. 7–8, fig. 1) are from the Crailsheim bonebed of the Upper Muschelkalk. Other material has been ascribed to this genus by Huene in 1922 (pp. 410–418, figs. 13–25) from the Lettenkohle (Lower Keuper) of Gailsdorf and Bibersfeld and by Schmidt in 1931 (pp. 261–266, pl. 4, figs. 21–27) from the Thuringian Lettenkohle, and by Broili (1927) from the Muschelkalk of Lower Franconia.

A portion of the skull table gives a number of elements in articulation, but otherwise the skull material is very fragmentary; in consequence there is considerable variation in the restorations given by Fraas in 1913 (fig. 1), Abel in 1919 (fig. 221), Huene in 1922 (figs. 13, 14) and Nilsson in 1937 (fig. 12). As far as it is known, the skull is of the type seen in the two preceding genera, but the anteroposterior compression of the skull table is even greater and it is possible that the shortening of the skull may have been more marked than we have indicated in our figure, which follows Huene here. As far as can be seen the skull elements are of the pattern seen in the last two genera; *Plagiosternum* is intermediate between *Gerrothorax* and *Plagiosaurus* in that the parietal appears to be expanded laterally sufficiently to reach to — or nearly to — the supratemporal. The jaw shows a highly developed retroarticular process.

The palate is unknown. The clavicles and interclavicle are present. As Nilsson points out, the original description of these elements by Fraas was erroneous in certain regards; the arrangement was apparently similar to that described for *Plagiosaurus*. Huene (1922, figs. 22–24) figures cylindrical centra, half as long as wide, with flat ends.

Plagiosuchus

(Fig. 40)

Founded by Huene (1922, pp. 418–425, figs. 26–28), the genus includes as its type "*Plagiosternum*" *pustuliferum* of Fraas (1896, p. 8) from the Lettenkohle of Gailsdorf; Schmidt in 1931 (pp. 269–270, pl. 4, figs. 29, 30) attributed to this species fragments from the Thuringian Lettenkohle. A second species, *P. pustuloglomeratus* (Huene 1922, 425–426, fig. 29), has as its type fragments from the Crailsheim bonebed of the Muschelkalk, and Schmidt (1931, pp. 266–269, fig. 40, pl. 4, fig. 28) assigned to this species as a "giant mutation" fragments from the Thuringian Lettenkohle. Very probably to be assigned to this genus are fragments from the Upper Muschelkalk of Lorraine, described by Corroy (1928, pp. 112–114, pl. 2, fig. 12, pl. 4, fig. 10) as *Plagiosternum perrini*, *Plagiosternum pustuliferum* and *Plagiosternum* sp. (as noted elsewhere, the type of *Nestorrhytias perrini* Meyer is apparently a capitosaur). This genus and *Plagiosternum* are geologically the oldest of the plagiosaurs. "*Plagiosternum*" *pustuliferum* was founded on shoulder girdle material. Our present knowledge of the form is based mainly on a slab from Gailsdorf, described by Huene, which contains much of the anterior part of a skeleton. The skull roof is unfortunately concealed. Much of the palate is visible and appears to agree fairly well with that of *Gerrothorax*. There is a prominent cluster of small teeth on the vomers. Portions of the jaw preserved agree with that of *Plagiosaurus*. The slab contains various postcranial elements such as an axis of typical stereospondyl build, and a primary shoulder girdle, the essential structure of which is similar to that of *Plagiosaurus*.

We may note in passing a perplexing set of three small vertebrae found with the type of "*Plagiosternum*" *pustuliferum* (Meyer and Plieninger 1844, pl. 7, figs. 5, 6; Huene 1922, p. 427, fig. 30). They are typically rhachitomous, with well-ossified pleurocentra; they are too small to belong to any adult capitosaur from these beds; but it is hard to believe, from what is known of other plagiosaurs, that they belong to a member of the present group.

Buettneria

(Figs. 12, 13, 41)

Turning to the metoposaurs, the most completely known, although one of the more recently described members of the group, is *Buettneria*

of the late Triassic of North America. Case has on various occasions (1922, pp. 13–25, figs. 1–5, pls. 1–4; 1924, p. 423, pls. 3, 4; 1931; 1932) described materials of this form from the Dockum beds of western Texas under the specific names of *B. jonesi*, *B. perfecta* and *B. bakeri*; Branson and Mehl have with doubt assigned to this genus a species, *B. major*, from the Upper Triassic Chinle formation of Arizona (1929, pp. 227–228); a large amount of material has been discovered in New Mexican deposits apparently equivalent to the Dockum (Romer 1939); Wilson (1941) has given a discussion of the endocranial anatomy; Sawin has published (1945) a comprehensive description of a new species from Texas, *B. howardensis*.

The generic validity of *Buettneria* and, indeed, of most genera of metoposaurs is questionable. As noted later, *Buettneria* differs but slightly from *Anaschisma*, earlier described from the western Triassic, and valid distinction from still earlier described genera of eastern North America is difficult to find.

Buettneria and its metoposaurid relatives have paralleled the capitosaur group in many features, such as a trend toward large size, large skulls, flattened heads and bodies and reduced limbs, indicating a purely water-dwelling existence of a sluggish type. As in the capitosaurs lateral line grooves are conspicuous.

The situation of the orbits, placed far anteriorly, is the most striking feature of the skull roof. It is frequently assumed that this situation implies a marked phylogenetic "reduction" of the anterior part of the skull and an elongation of the more posterior part. Actually, however, the major event may have been an anterior movement of the orbits. If the skull be compared with that of a capitosaur or neorhachitome of similar cranial outlines, it will be seen that there has been little shift of palatal structures or, as far as can be deduced, of those of the endocranium. It is the orbits alone that have shifted position. The dermal bone pattern of the skull roof has been modified to adjust to the new orbital position, with shortening of the anterior elements, and great elongation of those posterior to the orbit.

In relation to this anterior movement the lacrimal, which in most advanced labyrinthodonts had lost contact with the orbital margin, here enters the rim of this opening. The external nares are very large and are close together, as in brachyopids. The openings in the snout found in the capitosaurs, apparently for accommodation of the tips of the lower fangs, are absent; it has been suggested that the large metoposaur osseous narial opening accommodated these structures. The central area of the skull roof above the braincase has

moved but relatively little forward, so that the parietals are far back of the orbital region, and in *Buettneria* the orbits lie opposite the anterior end of the frontals rather than in their usual relative position opposite the posterior end of these bones.

The palate parallels that of the capitosaurs in the large vacuities and there is a broad fusion of the pterygoids with the basicranial region. Again as in capitosaurs the quadrate articulation has moved forward to a position nearly opposite the basal articulation. A contrast, however, with the capitosaurs is the fact that the cultriform process of the parasphenoid is much broadened (cf. plagiosaurs). Paired vacuities for lower jaw fangs are present anteriorly. In most regards the details of palatal construction appear to compare well with those seen in the capitosaurs. In *Buettneria*, however, the palatal vacuities are so enlarged that the pterygoid makes no contact with the palatine. The cultriform process extends far forward, flanked on either margin by posterior processes of the vomers (cf. *Batrachosuchus*). A characteristic palatal dentition comparable to that of the capitosaurs is present. The vomers bear tusk-pairs opposite the premaxillary-maxillary sutures; a transverse row of smaller teeth crosses between these fangs and a festoon of similar small teeth extends backward internal to the choana. A tusk-pair is present on the palatine lateral to the choana; thence a long series of small teeth runs backward along palatine and ectopterygoid.

The pterygoid meets the parsphenoid in a greatly elongated suture; posteriorly there is a powerful articulation of pterygoid with exoccipital, broadly visible on the ventral surface. Low transverse ridges on the posterior end of the parasphenoid are vestiges of basisphenoidal tubera. A canal for the internal carotid enters the substance of the parasphenoid posterolaterally, and runs some distance forward before emerging dorsally, whence the carotid presumably continued forward between parasphenoid and the cartilaginous floor of the braincase. A canal which enters the parasphenoid from above and runs forward in that bone more antero-laterally presumably carried the palatine vein.

The position of the basipterygoid process of the braincase — here, as in other Triassic genera, in a cartilaginous condition — is readily seen in Wilson's figure (1941, fig. 2). A well defined recess is visible in the medial surface of the base of the epipterygoid and the region of the pterygoid just adjacent posteriorly; this recess undoubtedly lodged the process; its proximal part is bounded posteriorly by a ridge on the upper surface of the parasphenoid.

The epipterygoid has a moderately expanded basal portion adjacent to the region of the basal articulation; a stout columnar ascending process; a short otic process. As Wilson notes, it is probable that the epipterygoid was continued in cartilaginous form over much of the inner (or lateral) surface of the pterygoid. He further describes in one specimen an area on the inner surface of the quadrate ramus of the pterygoid suggestive of an additional ossification (perichondral) of this palatoquadrate cartilage.

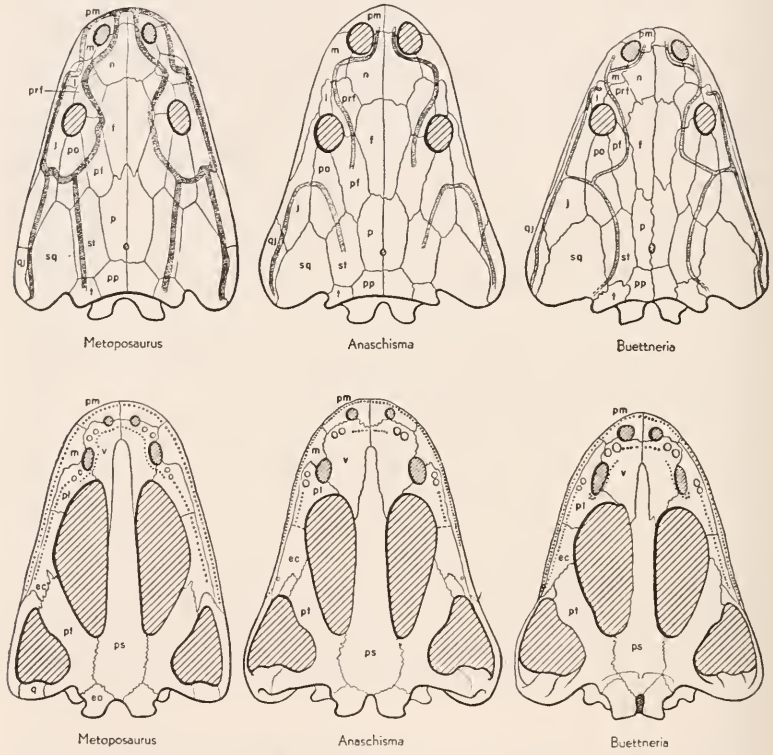

Fig. 41. Metoposaurs. *Metoposaurus* mainly after Fraas; *Anaschisma* after Branson and Mehl; *Buettneria* after Case.

The suspensorial region is of complex build and is currently not thoroughly understood. Distally there is a stout quadrate which extends proximally a short distance along the inner surface of the

pterygoid. The latter bone includes a structure — the "anterior rising process" of Case and of Wilson — which appears to correspond to a well-developed quadrate ramus. However, the bone turns backward and inward ventrally and produces another, lower, "rising process" posteriorly. Between the two processes there is an area filled either with matrix or spongy bone of uncertain identity. From above, a process of the squamosal descends broadly into this region,

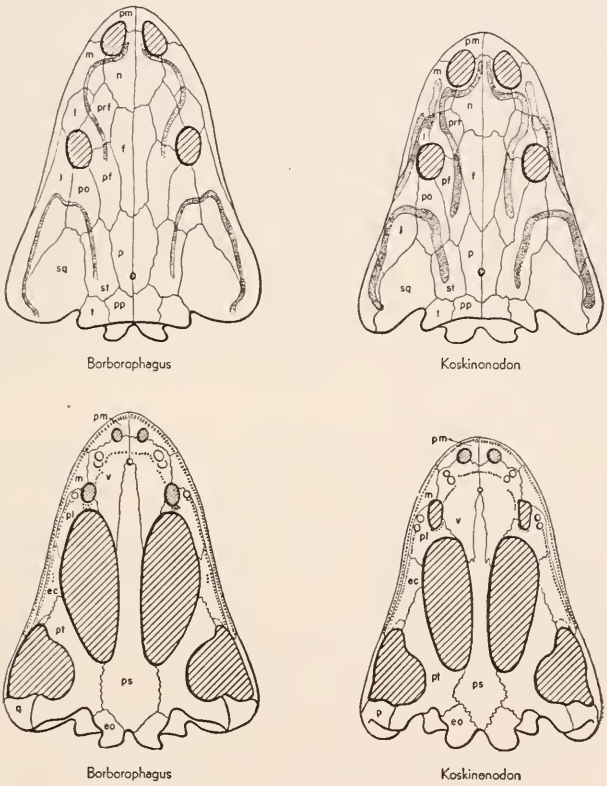

Fig. 42. American metoposaurs. After Branson and Mehl.

and this material may be an over-development of the somewhat similar, if smaller, squamosal buttress seen, for example, in *Edops*. Along the lateral part of the suspensorium, the skull roof is separated by a long oval fenestra from the palato-quadrate complex below it.

This fenestra is surrounded in great part by the squamosal and its descending flange; ventrally an extension from the quadratojugal forms much of its boundary.

In the braincase unossified gaps represent basioccipital and supraoccipital regions (a trace of bone may be present in the former area). Notable is the fact that in metoposaurs the posttemporal fossa is reduced to a small opening and there is no projecting paroccipital bar, but rather a broad vertically descending dermal flange formed in the main by the tabulars. The occiput slopes strongly backward ventrally, the paired condyles projecting markedly beyond the posterior margin of the skull roof. The exoccipitals extend upward to meet the descending dermal flanges and downward far anteriorly and laterally, enclosing the vagus foramen (the hypoglossal is absent) and forming floor and posterior wall for the otic region of the braincase. Apart from the exoccipitals the braincase was almost entirely cartilaginous. Wilson has described a partially ossified prootic in one specimen, but almost no other traces of otic, sphenoid or ethmoid ossifications have ever been described, and we can only make such inferences in braincase structure as can be deduced from the contours and markings of the adjacent dermal bones. There was an elongate bladelike stapes, lacking a stapedial foramen, but with a highly developed accessory head.

The lower jaw is relatively very deep, and in life presumably slanted strongly inward. There was a well developed retroarticular process, truncate posteriorly in outline. Case describes two coronoids, but one other metoposaur at least, is said to have had the usual three elements. Small teeth were present on the posterior coronoid, and the dentary bears internally in the symphysial region a fang pair and additional small teeth.

Almost no articulated postcranial material has been described, but isolated elements have been found in great abundance; some of them are described in various papers by Case, who has essayed a tentative reconstruction of the body form; Sawin has described a mounted skeleton. The cleithrum is small; the clavicle is considerably expanded dorsally (cf. plagiosaurs), but this expansion is unsculptured. The clavicles and interclavicle are broadly expanded ventrally. The interclavicle is truncated posteriorly, but all three elements are elongated anteriorly.

The vertebrae are definitely stereospondylous in the proper sense of the term. The centra are in the vast majority of known examples solid disc-shaped structures; there is no notochordal perforation

and there is even little trace of an amphicoelous condition; in fact some presumed dorsals show one somewhat convex face (the probable anterior surface) which appears to have fitted into the slightly concave posterior surface of the adjacent centrum, giving a reptile-like opisthocoelous condition. Many large "centra" (presumed dorsals) show a pronounced rib facet high up on the posterior margin, and a less pronounced indentation opposite on the anterior edge, suggesting that the capitular articulation was tending to assume an "intercentral" position, as in plagiosaurs. The anterior and posterior margins of the centra are parallel and vertical in side view, rather than showing the wedge-shape of capitosaurs, and demonstrate that no room existed between successive centra for even reduced or cartilaginous pleurocentra. There is no indication that the centrum is a compound structure, and it seems certain that it is an expanded and modified intercentrum. These centra have been described by Case, and similar centra from the Wyoming genera are well shown in photographs by Branson and Mehl (1929, pl. I). The dorsal surface of the centrum shows a longitudinal groove indicating the floor of the neural canal; lateral to it are roughened areas for the attachment of the neural arch; the exact nature of the connection is, however, unknown.

Anaschisma

(Fig. 41)

This genus, from the Popo Agie beds of the Chugwater (Upper Triassic) of western Wyoming, is known almost exclusively from the skulls (about half a meter in length) forming the types of two species, *A. browni* and *A. brachygnatha*. Originally described by Branson (1905), the material was redescribed by Branson and Mehl in 1929 (pp. 195–203, fig. 6, pls. 2, 3). As may be seen from the figures, the genus is essentially similar to *Buettneria*, although differing in detail, such as the less marked reduction of the anterior portion of the skull and a more posterior position of the orbits. In *Anaschisma* the ectopterygoid is described as very small; perhaps there has been confusion with the palatal area of the jugal.

In addition to *Anaschisma* Branson and Mehl (1929) have described two other genera of metoposaurids from the Popo Agie beds. They are seemingly closely related to one another and to *Anaschisma*. Differences described are slight. *Borborophagus wyomingensis* (Fig. 42) was founded on a small skull which differs from *Anaschisma* in

a longer and more pointed facial region and corresponding differences in palatal proportions; its describers further note that the dermal bones are very thin. *Koskinonodon princeps* (Fig. 42) has as a type a skull which is in general comparable to that of *Anaschisma* but which differs in various details. Branson and Mehl have described in this form a series of structures which they suggested might be an unusual type of auditory apparatus, but which appear to consist of the displaced and fractured epipterygoid in addition to the normal amphibian stapes. Also similar to *Anaschisma* is *Kalamoiketor pinkleyi*, known only from a partial skull from the Chinle formation of the late Triassic of Arizona. It was described by Branson and Mehl (1929), who noted that the bones were, as in *Borborophagus*, very thin, and that from the material known there is little to separate it from this last genus. They suggest that a metoposaurid interclavicle from Arizona described by Lucas (1904) as *Metoposaurus fraasi* may belong here.

There is little reason to believe that these forms are all generically distinct. *A priori*, it is none too probable that three closely related genera (*Anaschisma, Koskinonodon, Borborophagus*) existed at the same time in Wyoming. The thinness and delicate sculpturing of the skull elements which are the major features of distinction of *Borborophagus* and *Kalamoiketor* may be correlated with the fact that the unique skulls representing them were of relatively small size; presumably this supposed generic character is indicative of juvenility. It is highly probable that all these forms can be included in the genus *Anaschisma*, and the possibility that *Buettneria* is also synonymous is worthy of investigation.

Dictyocephalus

The metoposaurs described above are from Upper Triassic deposits of western North America. There appear, however, to be remains of this sort also from the Newark series of the Appalachian region. The material is poor and comparison with the better known western forms is difficult. It will be noted, however, that the two genera founded on such material were named much earlier than the western forms and thus have priority if identity should be established.

First described of eastern types was *Dictyocephalus elegans*, based by Leidy (1856, p. 256) on a partial skull from Chatham County, North Carolina. As figured by Emmons (1857, figs. 51, 52), this is definitely the post-orbital region of a metoposaur indistinguishable from the *Buettneria* type.

Eupelor

Later, Cope (1868, p. 221; 1893, p. 12, etc.) described *Eupelor durus* on the basis of a partial skull from Chester County, Pennsylvania; to this species he also assigned fragments from York County, Pennsylvania, and from the Upper Triassic of Texas. No figures of the original material have been published. The Texas material was obviously of the type now termed *Buettneria*. Huene (1921, p. 572, figs. 16–18) described as *Eupelor* some further fragments from the Newark series in York County, these consisting of a labyrinthine tooth and parts of two shoulder plates. Huene compared these plates with *Mastodonsaurus* (to which Cope had originally referred the *Eupelor* material); they are, however, very similar to *Buettneria*. *Calamops paludosus* from Bucks County, Pennsylvania, was described by Sinclair (1917), with part of a large jaw as the type. No details are given and there is no known way of distinguishing this form from *Eupelor* from the same group and region (or, indeed, from any other large labyrinthodont).

Metoposaurus

(Figs. 13, 41)

This genus (long known as *Metopias*) was one of the first described labyrinthodonts, but is still known from a relatively small number of specimens. Most of those assigned to the type species, *M. diagnosticus*, are from the Schilfsandstein of the Middle Keuper of the Stuttgart region; the best preserved specimens, including a large skull and a second with much of the skeleton, were described by Fraas (1889, pp. 137–156, pls. 12–16; 1896, p. 8, pl. 1; cf. Watson 1919, pp. 32–35, figs. 18–20). Further material from the Middle Keuper, including fragments of a smaller animal, was described by Fraas (1913, pp. 285–288, pl. 17, figs. 4, 5) as *M. stuttgartensis*; *M. sanctaecrucis* (Koken 1913, pp. 20–24, pls. 1, 2) is a skull from the roughly comparable Raibl beds of the South Tyrol; *M. heimi* (Kuhn 1932, pp. 112–119, pls. 4, 5, fig. 3) is a large skull from the Middle Keuper of Upper Franconia; Corroy (1928, pp. 110–111) states that specimens of *Metoposaurus* are present in the Lower Keuper of Lorraine; Miall (1875, p. 157) mentions a specimen from the Rhaetic of Bristol, but I am not aware of any further data on this report. Schmidt (1931,

pp. 258–261, fig. 6c, pl. 4, fig. 20) described, as *Trigonosternum latum*, a triangular interclavicular impression from the Thuringian Lettenkohle which he believed to be that of a new metoposaur. But it is obvious that the bone is incomplete and it may be half of a normal *Metoposaurus* interclavicle broken somewhat to one side of the center.

Certain details of palatal construction are not too clear, but for the most part the skull pattern, both dorsally and ventrally, is clearly comparable to that seen in the American genera. A difference worthy of note is the fact that the lacrimal does not enter the orbital margin; further, post-orbital elongation is even greater in *Metoposaurus*, but facial reduction is not as great.

The occiput, as described by Fraas, Watson and Kuhn agrees well with that of the American genera. Little is known of the internal structure apart from an exoccipital described by Huene (1922, pp. 396–400, fig. 17) and some data regarding pterygoid and parasphenoid noted by Watson.

A considerable part of the anterior portion of the skeleton was present in one of Fraas' specimens. As far as preserved, the individual elements show, for the most part, good agreement with those of *Buettneria* and in addition are found in articulated condition, giving us the outlines of a broad, flat trunk. Of the limbs only a humerus is preserved. This is incompletely ossified and featureless; its size indicates that the limbs were relatively weak. The one conspicuous difference between this specimen and its American relatives lies in the vertebral structure. As we have noted, the American forms have heavily ossified "centra". In this specimen these elements are simply hemicylinders of no great thickness, although with parallel anterior and posterior margins, rather than the triangular shape of primitive intercentra or those of capitosaurs as seen in side view. It is reasonable to believe that there was present in cartilage a solid "centrum" similar to that of *Buettneria*. Whether the incomplete ossification is a generic or, as one may suspect, an age character cannot be said.

INDIAN METOPOSAURS

Huene (1940, pp. 1–5, pl. 1) has recently described remains of metoposaurs from the Upper Triassic Maleri beds of India. Three types appear to be represented, but the material is too fragmentary for systematic description.

DISCUSSION

It seems certain that the genera first reviewed in this section — *Bothriceps, Brachyops, Batrachosuchus, Pelorocephalus,* and ? *Tungussogyrinus* — are closely related forms to be included in a Family Brachyopidae; this conclusion was reached by Broom in 1915, and has been agreed to by all later workers on the group — Watson (1919, p. 68), Huene (1922, pp. 442–446) and Nilsson (1937, p. 57). We may first consider these types and their origin without reference to the later and more specialized plagiosaurs.

Bothriceps, Brachyops, Batrachosuchus and *Pelorocephalus* show, to an increasing degree, the development of a peculiar short-faced, broad-skulled type from a skull of the "central" type seen in various rhachitomes. All show, as well, the marked backward slant of the occiput which, together with forward movement of the jaw articulation, may be interpreted as an adaptation for easier elevation of the skull and opening of the mouth in these depressed forms. There are, unfortunately, no postcranial remains of any sort definitely associated with adult specimens, so that we have no direct evidence of vertebral structure or of body and limb specializations which one may reasonably assume to have accompanied the specialization of the skull. There is, however, evidence for the possession by the brachyopids of ring-shaped stereospondylous vertebral "centra".

Watson in 1919 (p. 56) suggested that these forms have descended from *Dvinosaurus* of the Russian Upper Permian; later workers, including Nilsson, agree in general, although the latter points out that the brachyopids cannot be descended directly from *Dvinosaurus* because of certain specializations seen in that form. The general skull proportions are similar in the two cases, although *Dvinosaurus* is actually shorter in the post-orbital region than *Bothriceps* and with the posterior elements of the table more reduced. In the palate there is, of course, a major difference in that *Dvinosaurus* has retained a movable basipterygoid articulation. *Dvinosaurus* has a very highly developed branchial arch skeleton, unknown in either brachyopids or the later plagiosaurs. Seemingly a major difficulty is the topography of the post-orbital region. As we have noted, *Dvinosaurus* technically lacks an intertemporal, but the reduction process has occurred in such a way that parietal and postorbital are broadly in contact, postfrontal and supratemporal separated; the brachyopids, on the contrary, have the normal pattern of the more advanced rhachitomes. It seems more reasonable to consider that the resem-

blance between *Dvinosaurus* and the brachyopids — mainly in facial abbreviation — is due to parallelism, and that the brachyopids are derived from neorhachitomes of the later Permian and Eotriassic.

Despite the evident contrasts, the brachyopid skull merits comparison with that of the metoposaurs. The brachyopids became progressively short-skulled, the latter elongate; but it may be noted that the relative length of pre- and post-orbital regions is similar in the two cases; the post-orbital segment is nearly twice that of the facial region. In both, the parietals are relatively more elongate than in most labyrinthodonts and the pineal opening is far posterior to the orbits. In both the cultriform process of the parasphenoid is very broad; in both — and in contrast with almost all other advanced temnospondyls — the exoccipitals are in broad contact ventrally with the pterygoids. In both the occiput projects backward from the skull roof to a marked degree. These features suggest a real relationship of metoposaurs and brachyopids.

The brachyopids are all from beds of early or mid-Triassic age, and are thus suitably intermediate in time of occurrence between possible Permian ancestors and the plagiosaurids.

The four genera next described — *Gerrothorax*, *Plagiosaurus*, *Plagiosternum* and *Plagiosuchus* — are obviously close to one another structurally and form a natural group, the Plagiosauridae. They are restricted in distribution — all are from central Europe, all from the latter half of the Triassic. Between the various specimens we can obtain a fairly complete description of the head and anterior part of the trunk of a curious type of amphibian. They were forms of moderate size, measuring a foot or so across the body, which was greatly flattened and but a few inches in depth. Limbs of modest size were present. The body shape, together with the presence of lateral line grooves on the skull, indicates that these forms were persistent water dwellers. It is a fair assumption that they were perennibranchiate, although the absence of ossified remains of gill bars suggests that the internal gills were not highly developed. They were well armored both ventrally and dorsally against larger or more active enemies. The body terminated abruptly anteriorly in a grotesquely short flat skull, with a broadly gaping mouth.

The general habitus of the plagiosaurs is reminiscent of *Diplocaulus* among the lepospondylous amphibians of the Permian; Jaekel, indeed, believed them to be related. Watson first suggested that they were labyrinthodonts related to the brachyopids of the earlier Triassic; later workers on these forms, Huene and Nilsson, have concurred

in this belief. Watson placed the plagiosaurs in the family Brachyopidae. Huene, however, erected a separate family, the Plagiosauridae, for these late Triassic genera, uniting Plagiosauridae and Brachyopidae in a super-familial group; in this he has been followed by Nilsson.

In the comparison of brachyopids and plagiosaurs only cranial anatomy is available since the postcranial structure of the former is unknown. As far as the evidence goes, however, there is no reason to doubt the possibility that plagiosaurs are descended from brachyopids. The skull shortening which reaches its extreme in the plagiosaurs is already advanced in *Batrachosuchus*; the palatal construction of that genus is one which may be considered antecedent to the plagiosaur condition.

Since nothing definite is known of the postcranial skeleton of the Brachyopidae, the data obtained from the Plagiosauridae regarding vertebrae and appendicular elements may be considered in regard to the ancestry of the group as a whole. The build of the vertebrae is puzzling. As we have noted, the plagiosaur centra are rather elongate, solid structures without notch or perforation for the notochord, with a double facet for rib articulation and an intervertebral position of the neural arch. These features contrast with typical stereospondyl conditions, although recent workers, such as Nilsson, assume that the centra are derived from the intercentral elements of more primitive forms, and presumably from typical rhachitomous intercentra. No closely comparable structures are seen in other Triassic types. The stereospondylous condition in which the intercentra form complete rings is found otherwise only in advanced capitosaurs and, particularly, in the metoposaurs.

The extreme expansion of the dermal shoulder girdle is a specialization of the group. The interclavicle is abruptly truncate posteriorly, and tapers to some degree anteriorly; the two clavicles meet one another broadly anterior to the interclavicle. This is a condition not found in "typical" rhachitomes or their Triassic capitosaur descendants; in them the clavicles usually do not come in contact, and the interclavicles tend to extend back of the posterior end of the clavicles to a variable degree. On the other hand, the metoposaurids show features comparable to the plagiosaur condition, for the interclavicle tends to be rather short posteriorly, and the clavicles to meet one another in front of the interclavicle.

Neither in vertebral structure nor in the dermal girdle does *Dvinosaurus* in any way forecast plagiosaur conditions (cf. Nilsson 1937l p. 63; 1939, pp. 22–23). The vertebrae in that genus are of norma,

rhachitomous construction, and although there may be fusion of central elements, the result of this fusion does not appear to give any closer resemblance to the plagiosaur "centra". And as regards the dermal girdle, *Dvinosaurus* is notable for a relatively unexpanded ventral area and for the development of a stem on the interclavicle, rather than reduction in its length.

On the other hand, we have noted in both vertebrae and dermal girdle resemblances between plagiosaurs and metoposaurs. These are slight in nature but, taken together with seemingly significant features of cranial anatomy mentioned earlier, seem to suggest a real relationship between metoposaurs and brachyopoids, and a common ancestry arising from Permian neorhachitomous forms.

It is indisputable that the metoposaurs form a compact group of genera, between which there are but minor generic differences, and which have many common features contrasting strongly with other labyrinthodonts. There are, actually, only two distinguishable generic types (apart from the Indian forms with which I am not familiar), *Metoposaurus* and an American series of forms, most or all of which may prove to be identical with *Dictyocephalus*.

The striking feature of the metoposaurs is, of course, the great elongation of the post-orbital region of the skull, combined with the retention of a relatively short face. The skull, again, is extremely broad and flat, to a degree unparalleled in other well-known groups except the plagiosaurs. The osseous external nares, which lie close together, are much enlarged and may have accommodated the tips of the lower jaw tusks as well as the narial structures. The otic notch is much reduced, so that there is a broad union of squamosal and tabular. The posterior portion of the palate is comparable to that of the plagiosaurs and in contrast with that of the trematosaurs and most capitosaurs in that there is a broad ventral contact between pterygoid and exoccipitals; comparable to certain capitosaurs and *Batrachosuchus* and in contrast with trematosaurs is the long exposure of the anterior end of the cultriform process. Contrasting with both trematosaurs and capitosaurs but in agreement with the plagiosaurs is the extreme breadth of this process. The palatal dentition is a simple variant of the type seen in other Triassic families, including the neorhachitomes, trematosaurs and capitosaurs. The posterior fenestra above the quadrate ramus of the pterygoid is an unusual feature, not known elsewhere except perhaps in brachyopids. This region of the pterygoid is, as noted, unusual in its construction. The extreme degree of reduction of braincase ossification, except for the

highly developed exoccipitals, is unmatched in other Triassic forms (the plagiosaurs, however, are undescribed in this regard). The marked posterior projection of the occiput is without parallel except in the brachyopids and plagiosaurs.

Postcranially, the vertebrae are distinctive. The intercentra, when fully ossified, as in *Buettneria*, are seen to be solid discs with abutting margins, without room for pleurocentral elements; this is in contrast to the capitosaur condition in which vestigial pleurocentra may have persisted in most cases. The interclavicle is, as might be expected, broad; the long contact between clavicles anteriorly is a distinctive feature, as is the dorsal expansion of these elements, a feature known otherwise only in plagiosaurs. The limbs, as far as known, are small and poorly ossified.

It seems certain that the metoposaurs were relatively sluggish bottom-dwellers, presumably feeders on a variety of fresh-water inhabitants; the highly developed tusks suggest that part, at least, of their prey must have been animals of good size. Suggestive of their habits is the nature of a find reported by the writer (1939) in which the remains of scores, and probably hundreds of animals, were crowded together in a small area. This probably was the last surviving pool of a series of ponds or lakes in which these animals had lived; drought had apparently caused them to collect in this fashion; they were unable to leave the drying pool to seek another dwelling place.

A majority of these forms are, we have seen, American types. Here they have a monopoly in the late Triassic amphibian fauna, whereas in Europe *Metoposaurus* is the sole — and relatively rare — representative, and metoposaurs were unreported elsewhere until the recent description of Indian specimens. This may mean that America was their homeland; but their abundance here may be due merely to lack of competition (the bison is a parallel case).

Their geological distribution is strictly limited. *Metoposaurus* is known only in the Keuper. The American and Indian forms are known only in Upper Triassic formations which are presumed Keuper equivalents.

In contrast to the contemporary capitosaurs, which can be readily derived from a neorhachitomous stock, the ancestry of the metoposaurs is none too readily discernible. One is, of course, immediately impressed with the superficial comparison with *Trimerorhachis*, in which pre- and post-orbital segments of the skull are similarly proportioned, in which the skull is already much depressed (despite its relatively early age), interpterygoid vacuities already much enlarged, and a

comparable palatal dentition already developed. This comparison has so impressed Säve-Söderbergh (1935, p. 90) that he includes *Trimerorhachis* with the metoposaurs in a common superfamily, Metoposauroidea. He gives a long diagnosis of the superfamily which, when analyzed, is seen to include no facts other than the obvious similarity in orbital position.

Trimerorhachis exhibits a number of features in which it is in advance of most genera of its age and is in a condition already approaching the metoposaurs — and other Triassic forms. The skull is greatly flattened; endochondral ossification greatly reduced; interpterygoid vacuities much enlarged; rows of palatal teeth developed; the body flattened and limbs reduced in size. All these are features to be expected in an ancestor of the metoposaurs. All, however, are also present in the neorhachitomes. And, further, the neorhachitomes approach the metoposaurs much more closely in a number of significant features in which they are far advanced over *Trimerorhachis*. The intertemporal, persistent in *Trimerorhachis*, is lost in the neorhachitomes; the basal articulation, movable in *Trimerorhachis*, is broadly fused in neorhachitomes; the occipital condyle, persistently single in the early Permian genus, is double in the neorhachitomes; Wilson (1941, p. 109) notes that there are no particular resemblances between the internal cranial structures of *Trimerorhachis* and those of metoposaurs.

The metoposaurs certainly demonstrate the existence of parallelism in the evolution of the labyrinthodonts. It is, however, much more reasonable, on present evidence, to believe that the parallelism lies between *Trimerorhachis* and the metoposaurs in the change in orbital position, rather than the more improbable assumption that a number of other significant features of Triassic amphibians were developed independently in *Trimerorhachis* descendants.

There are, as we have said, no known forms clearly and directly antecedent to the metoposaurs. If we attempt to tie them in to the trimerorhachids, we find a time gap of nearly two periods, from the earliest Permian to late Triassic, in which no possible intermediates are present except perhaps the poorly known *Chalcosaurus*. Nor is the transition from the neorhachitomes apparent. Most such forms exhibit elongation, rather than relative shortening, of the snout. However, the South African neorhachitomes exhibit skull proportions of the "normal" type from which the trimerorhachid and metoposaurid configuration has surely been derived. The period between late Permian and late Triassic is sufficient for the evolutionary shift in orbital position.

The possible annectant nature of the brachyopids deserves consideration. These early Triassic forms are usually considered as leading solely to the plagiosaurs. It may well be, however, that they are also close to the line of ascent of metoposaurs from the neorhachitomes of the Eotriassic. *Bothriceps* and *Brachyops* are short-faced, but not shortened post-orbitally.

We have noted in our discussion of brachyopids, plagiosaurs and metoposaurs a number of common distinctive features which are apparently significant: highly developed stereospondylous "centra"; great flattening of skull; apposition of the external nares; reduction of otic notch; wide cultriform process of parasphenoid, broadly exposed anteriorly; great elongation of pterygoid contact with both excessively wide parasphenoid and exoccipital ventrally; reduction of posttemporal fossae. These features strongly indicate that brachyopids, plagiosaurs and metoposaurs are related forms which may be included in a common superfamily, the Brachyopoidea.

ANURAN ANCESTRY

The Anura, although not to be included among the Labyrinthodontia, are generally assumed to have originated from this group of early amphibians, and a brief discussion of their relationships seems appropriate.

The pre-Jurassic history of the frogs was quite unknown until the recent discovery by Piveteau (1937) of a Triassic amphibian from Madagascar in which a characteristic anuran skull was developed, but the postcranial skeleton had not yet attained the frog condition. More recently Watson (1940) has described the small amphibians *Amphibamus grandiceps* and *Miobatrachus romeri* from the Pennsylvanian of Mazon Creek, Illinois, and has reasonably argued that they represent early anuran ancestors. He includes them in the "Order Phyllospondyli", although admitting that they are not closely allied to other members of this supposed group. As I have pointed out elsewhere, the phyllospondyls are to be regarded as being for the most part larval labyrinthodonts, and Watson's argument confirms, therefore, older beliefs in the derivation of the Anura from labyrinthodont ancestors.

In the skull of *Miobatrachus* (Fig. 43) or *Amphibamus*, many features of the pattern are comparable to those seen in labyrinthodonts, particularly in young or presumably paedogenetic forms in

which the skull is short and broad, the otic notches large and the suspensorium well forward. However in certain notable features which Watson reasonably interprets as foreshadowing anuran conditions, *Miobatrachus* has already departed far from the labyrinthodonts.

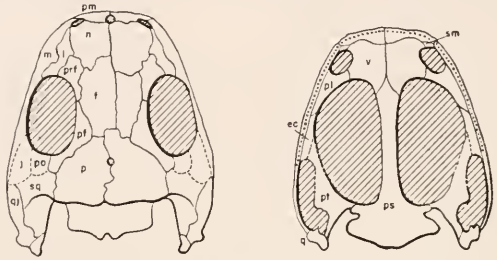

Fig. 43. The primitive "frog" *Miobatrachus*. After Watson.

These features have to do particularly with the loss of the two temporal bones and of the posterior elements of the skull table; the last results in the dorsal exposure of the broad braincase. The absence of the elements just mentioned removes from consideration criteria useful in determining whether these forms are more closely related to the temnospondyls on the one hand, or to the anthracosaurs on the other. As suggesting, however, relationship to the temnospondyls rather than embolomeres, we may note the firm union of the lateral wall of skull roof and table anterior to the large otic notch, and on the palate the broad vomers widely separating the choanae as in temnospondyls. Despite the fact that there is a retention of movable basipterygoid processes, the interpterygoid vacuities are large; a condition which developed rather rapidly in the temnospondyls, and not in anthracosaurs.

Posteranially, many features are primitive in nature and resemble labyrinthodonts in general rather than any specific group. However, the short unstemmed interclavicle suggests the temnospondyls; the phalangeal formula appears to have been low, and there are but four digits in the manus, as in temnospondyls. In the vertebral column the intercentrum is, as in temnospondyls, a ventral crescent; the pleurocentra are ill-known, but were certainly not the well-formed cylinders of the anthracosaurs. The caudals, Watson notes, have a typically rhachitomous appearance.

The evidence thus strongly suggests a derivation of the Anura from primitive rhachitomous temnospondyls. Except for the loss

of dermal roof elements, *Amphibamus* and *Miobatrachus* might well be regarded as members of the stock of Carboniferous rhachitomes of which *Eugyrinus*, *Pelion* etc. are members. This is in complete agreement with Watson's beliefs as to relationships, although differing radically in the taxonomic scheme employed. The *Eugyrinus* group does not appear until the typical Coal Measures; *Amphibamus* and *Miobatrachus* are from a late Westphalian locality. It is possible that the divergence of the amphibamid group from the rhachitomes took place at some time in the early part of the Pennsylvanian.

EMBOLOMERES

We now enter upon a discussion of the second major group of labyrinthodonts, here termed the Anthracosauria, and including the Seymouriamorpha as well as the Embolomeri discussed in the present section.

The embolomeres are an ancient and primitive group of amphibians; their structural features and their relationships are discussed below. Genera included here are: *Pteroplax*, *Ichthyerpeton*, *Pholiderpeton*, *?Memonomenos*, *?Nummulosaurus*, *Archeria*, *Cricotus*, *Eobaphetes*, *Spondylerpeton*, *Calligenethlon*, *Pholidogaster*, *Palaeogyrinus*, *Anthracosaurus*, *?Crassigyrinus*, *Papposaurus* and *?Eosaurus*.

Pteroplax

(Figs. 9, 12, 44, 45)

Best known of embolomeres and characteristic of the typical, late members of the group is this form common in the Coal Measures of Great Britain. It was frequently (but erroneously) called *Anthracosaurus*, as well as a variety of other names by early writers, and has recently been thoroughly described as *Eogyrinus attheyi* by Watson; the oldest available name, however, appears to be *Pteroplax cornutus*. Pertinent literature includes: Hancock and Atthey 1868, pp. 266–276, pls. 14, 15, figs. 1, 2; 1870, pp. 378–379; 1871, pp. 76–77; Barkas 1873 in part; Atthey 1876, 1877; Embleton 1889; Lydekker 1890, pp. 159, 160; Watson 1912a; 1926, pp. 222–238, figs. 18–25.

Most of the material, including that described by Watson and the earlier writers listed, was derived from the Lower Main Seam of Newsham, near Newcastle, collected principally by Thomas Atthey during the late '60's and '70's. Watson also notes the presence of

this genus from the Yorkian of the Rag Mine Ironstone of Staffordshire, and it or a very similar animal appears to have been common in Ireland (see *Ichthyerpeton*). As noted above, *Pteroplax* appears to be the oldest available name. Watson points out that the type of *P. cornutus*, while otherwise indistinguishable from the remainder of the material, differs in details of the tabular horns, and for this reason he coined the new term *Eogyrinus* for the mass of the material. This difference in construction, however, appears to be a minor variation. As Watson notes, most references in the literature to *Anthracosaurus russelli* have to do with the present form rather than with that rare genus.

Pteroplax was a large animal, with a skull length of about 40 cm. The roof pattern is completely known. The skull was relatively elongate and rather narrow in the pre-orbital region, suggestive of a piscivorous existence analagous to that of various temnospondyls of the Permian and Triassic. These contours are equally characteristic of other embolomere genera of the later Pennsylvanian and early Permian. Lateral line grooves are present on both skull and jaw. Presumably in relation to facial elongation, the lacrimal fails to cover its original territory from orbit to narial region.

The region of the skull table shows characteristic anthracosaur and embolomere features. A simple diagnostic character of both embolomeres and seymouriamorphs which readily distinguishes them from temnospondyls is the relatively large tabular, which has a broad contact with the parietal. The intertemporal persists, as in all anthracosaurs, and in the more typical embolomeres extends forward nearly to the orbital margin so as almost to separate postfrontal and postorbital. The table and cheek are but loosely united along a line leading forward from the slit-like otic notch, so that specimens tend to be disarticulated here; this construction is reasonably interpreted as a primitive character, held over from crossopterygian ancestors. Well developed tabular "horns" — spike-like posterior projections — are a characteristic embolomere feature. Watson believes these to have articulated, *via* a posttemporal element, with the shoulder girdle. But, as noted later, there is no certain evidence of the existence of such a bone; and it is perhaps more probable that such a connection was a ligamentous one.

The palate was primitive in nature, resembling that of early temnospondyls in such features as the closed interpterygoid vacuities and movable basal articulation. There are in addition definitely anthracosaurian characteristics. Diagnostic is the fact that the

choanae are far forward and closer to one another than is true of temnospondyls. In relation to this, the vomers are narrow and in known embolomeres fail to carry the pair of tusks common on this bone in temnospondyls. In *Pteroplax*, as in embolomeres generally, the palatine carries a well-developed fang-pair, and the ectopterygoid a principal pair followed by teeth of smaller size.

The braincase is present, but incompletely preserved; braincase structure in embolomeres is discussed in the account of *Palaeogyrinus*. We may note here that comparison of these two forms suggests that the large bony mass which Watson identifies in *Pteroplax* as the exoccipital appears, by comparison with *Palaeogyrinus*, to be more probably the opisthotic, the small exoccipital having been lost. Under this interpretation, *Pteroplax*, unlike *Palaeogyrinus*, appears to have had a normal fenestra ovalis — namely, the opening which Watson identified as the vagus foramen, but which is too large and too far forward to be, to my mind, interpreted as such.

The jaw is of a type found in a number of other embolomeres. It is deep posteriorly, but tapers markedly anteriorly. The marginal teeth on both upper and lower jaws are rather small and close set. As in other known anthracosaurs, there are no symphysial dentary fangs. There are three toothed coronoids, and a very long prearticular. A typical embolomere feature is the presence of two greatly enlarged meckelian fossae, lying below the prearticular and separated by a slender postsplenial bar. There is no retroarticular process.

The vertebral column is adequately known, not only from isolated vertebrae, but also from an articulated column; this was early figured by Barkas (as "*Macrosaurus*"), Atthey and Embleton (as "*Loxomma*"), and redescribed by Watson. There are 26 presacrals preserved, and the total may have been considerably higher. The animal may have measured 7 feet to the pelvis, with a total length of perhaps 15 feet. The neural spines are well-developed, the arches (in contrast to seymouriamorphans) not expanded, the zygapophyses close to the mid-line. The vertebrae are typically embolomerous, both intercentra and true centra (pleurocentra) being complete discs. However, in contrast to *Archeria* ("*Cricotus*"), the best known American form, the intercentra are not only slender but especially thin dorsally — perhaps a primitive condition. Dorsal ribs preserved are long, curved, and distinctly two-headed, the tuberculum forming a prominent shoulder at some distance from the capitular extremity of the rib. There is at present no evidence of the single expanded

sacral rib common in amphibians; *Pteroplax* shows three peculiarly expanded ribs, with which, Watson suggests, the ilium may have had a ligamentous connection rather than a firm union; if confirmed, this would appear to be a primitive condition.

Watson describes and tentatively associates with *Pteroplax* a shoulder girdle from Newsham with very broad dermal elements and a relatively small "primary" girdle. But there is no proof of the association; other related embolomeres have a rather normal girdle

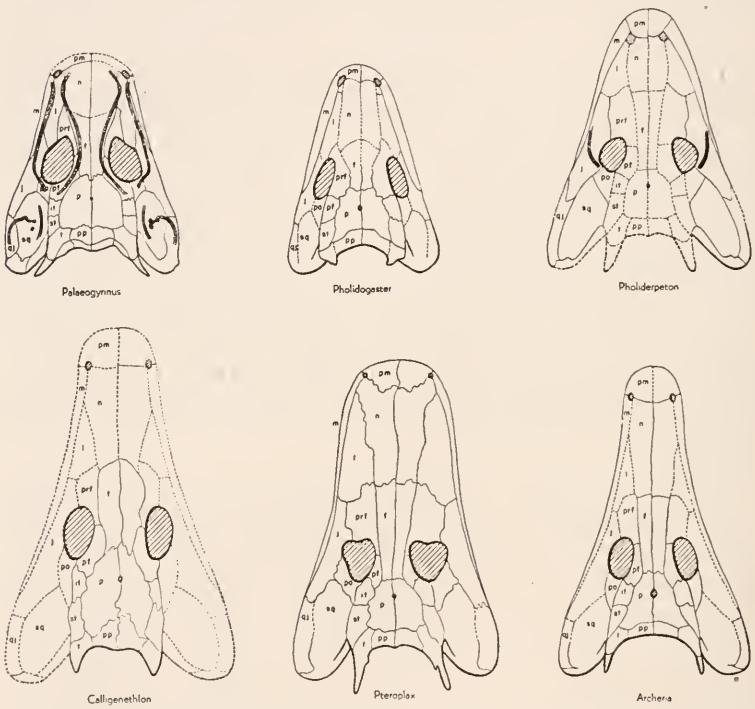

Fig. 44. Skull roofs of embolomeres. *Palaeogyrinus, Pholidogaster, Pholiderpeton* after Watson; *Calligenethlon* after Steen; *Pteroplax* after Atthey; *Archeria* partly after Broom. In *Pholidogaster,* prf = prf + pf; pf = it.

of amphibian type, and it is quite possible that this girdle pertains to one of the larger Carboniferous crossopterygians.

Hancock and Atthey (1868, p. 277) note the presence at Newsham of a rhomboidal interclavicle with the posterior tip produced as a

short blunt stem. This bone presumably belongs to either *Pteroplax* or *Megalocephalus*, and seems to have been of a typical embolomere structure; cf. those noted under *Crassigyrinus* and *Archeria*.

No pelvis is associated, but presumably that of *Pteroplax* was similar to the pelvic girdle seen in other embolomeres. In them there was a well-ossified pubo-ischiadic plate and the usual type of acetabulum. Above the acetabulum there was an iliac blade of modest size; more prominent, however, was a long, posteriorly-

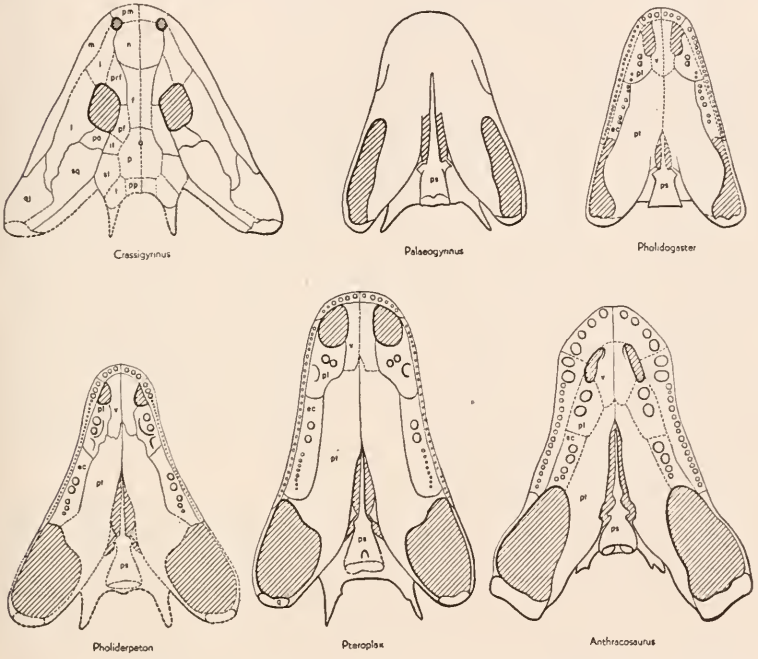

Fig. 45. Embolomeres. *Crassigyrinus, Palaeogyrinus, Pholidogaster, Pholiderpeton, Anthracosaurus* after Watson; *Pteroplax* after Atthey, Watson.

pointing rod-like extension of the ilium. Except for a small femur, indicating that the legs were small, there are no associated limb-bones.

Restored, *Pteroplax* shows a long, slender body, terminating in a long, seemingly compressed and obviously powerful tail which was the main swimming organ. Its whole organization was very

similar to "*Cricotus*" of the American early Permian. *Pteroplax* was surely an aquatic animal, presumably piscivorous in habits, and would have had much the appearance of a crocodile.

Ichthyerpeton

There is considerable evidence of the presence of seemingly close relatives of *Pteroplax*, including animals of large size, in the famous Jarrow (Kilkenny, Ireland) Coal Measures deposits.

The only adequately described remains consist of the partial skeleton to which Huxley (1867, pp. 367–368, pl. 23, fig. 1) gave the name *Ichthyerpeton bradleyae*.[1] This was a relatively small animal. The specimen (seen in side view) lacks the head and pectoral regions but includes much of the trunk and tail. There are about 25 presacrals preserved, and it is obvious that a considerably higher number.— ?35 or more — must have been present in the complete presacral column. There is a well developed ventral armor and evidence of a complete scaly covering of the tail and dorsal region. The tail was obviously an elongate and powerful structure. Huxley notes the discoidal shape of the vertebral centra. Lydekker (1890, pp. 168–170) states that the vertebrae "do not appear to be of an embolomerous nature", but the appearance of the specimen suggests the contrary, although the nature of preservation of the Jarrow material prevents accurate determination. It seems reasonable to believe that we have in *Ichthyerpeton* a typical Carboniferous embolomere of the widespread *Pteroplax-Archeria* group.

No further Jarrow embolomere material has been figured, but there are positive indications of the presence of larger embolomeres of this sort. In Huxley's paper on the Jarrow fauna he notes in a postscript (Huxley 1867, p. 369) evidence of "a large amphibian, closely allied to, if not identical with, the *Anthracosaurus*" (*i.e.*, *Pteroplax*), and lists the generic term *Discospondylus*. This genus was never described, but obviously was intended to apply to disc-shaped — and hence presumably embolomerous — vertebrae. Lydekker in 1890 (p. 159) cites from Jarrow, as "*Anthracosaurus*", vertebrae and a partial vertebral column of this type. Baily (1879, 1884) describes (but unfortunately does not figure) further large specimens, referring them to "*Anthracosaurus*". Specimens specifically described as *A. edgei* were estimated to have been 6–10 feet long in life, with a triangular head 12–14 inches long. This species is stated to be similar

[1] "*Ichthyerpeton*" *squamosum* of Moodie (1916, p. 135) does not belong to this genus.

to "*Anthracosaurus russelli*" — i.e., *Pteroplax*. One specimen includes a vertebral column of 60 segments with a deficient tail; the hind legs were about 4½ feet from the snout, indicating a presacral column of 30 or so vertebrae. There thus appears to be little doubt that at Jarrow, as at various other Pennsylvanian localities in the British Isles, there was present an embolomere closely related to, if not identical with *Pteroplax*, and the *Ichthyerpeton* type may well be a small, immature representative of this form.

Pholiderpeton

(Figs. 44, 45)

A skeleton from the typical Coal Measures of Bradford, Yorkshire, is the type of *Pholiderpeton scutigerum* (Huxley 1869; Watson 1929, pp. 222–224, figs. 1, 2). The specimen was apparently a complete skeleton, but more or less disarticulated; part, including the shoulder region, has been lost, and the remainder is not in too good condition. As may be seen from Huxley's and Watson's figures, little can be made of the skull roof and nothing of the palate; as far as can be seen the general structure is comparable to that of *Pteroplax*, as is the external surface of the jaw (which is slender at the symphysial end and rapidly deepens posteriorly). There are typical embolomerous central elements and masses of ventral scutes. There are no describable remains of limbs or girdles except a shoulder element which Watson (1926, pp. 234–235, fig. 26) suggested to have been a posttemporal. It is, however, of appropriate shape for an embolomerous cleithrum, and resembles that of *Archeria*. It will be noted that despite the suggestive presence of tabular "horns" in embolomeres, there is, apart from this bone just mentioned, no evidence of any element in any labyrinthodont yet described which connected skull table with shoulder in piscine fashion.

Watson (1929, pp. 223–224, fig. 2, pl. 1) has associated with *Pholiderpeton*, as specifically identical, a skull and jaws from Airdrie, Scotland. This is from a considerably earlier (Lanarkian) level in the Carboniferous, and specific and even generic identity is far from certain. This specimen, however, is seemingly of the same general type, and shows clearly the *Pteroplax* mandibular construction, with two large internal fenestrations. As in *Pholiderpeton* and other members of this group, we find a slender snout and anthracosauroid conditions in the narrow toothless vomers.

It is obvious that *Pholiderpeton* is a typical Pennsylvanian embolomere, closely related to *Pteroplax*.

Memonomenos

(Fig. 46)

The only specimen representing *M. dyscriton* is a badly preserved skull and dermal shoulder girdle from Košťálov, Bohemia, a locality believed to be basal Permian; the specimen was noted by Fritsch, but first described by Steen (1938, p. 240, fig. 26). This is a long-skulled type with slender proportions and centrally situated orbits. There appears to have been an intertemporal, but the outlines are uncertain; the tabular is large and appears to have had a contact with the parietal; it bears a small "horn". While the material is none too satisfactory, it seems likely that we are dealing with a late-surviving European embolomere, contemporary with *Archeria* of North America.

At Kounová, a Bohemian locality of slightly earlier age (perhaps just below the Stephanian-Autunian boundary) there are fragmentary remains of a typical embolomere, including vertebrae and characteristic pelves (Fritsch 1901, pl. 66, figs. 1, 2, 45; pl. 67, figs. 1, 2; pl. 69, fig. 8). These were originally referred, in the main, to *Macromerion*, a name which may be best applied to a pelycosaur; I have provisionally referred them, as *Memonomenos simplex*, to the present genus (Romer 1945, pp. 424–425).

Nummulosaurus

N. kolbii (Fritsch 1901, pp. 189–190, pl. 162, figs. 5–8) consists only of part of a tail of a small amphibian from Třemošná, Bohemia, a locality close to the Westphalian-Stephanian boundary. The vertebrae, as seen from the side, appear to be those of an embolomere; the only other material consists of small rounded but apparently overlapping caudal scales. There is, however, no guarantee that the genus is not identical with the seymouriamorph *Diplovertebron*, in which the vertebrae are similar in side view.

Archeria

(Figs. 12, 14, 44)

Above we have reviewed the evidence for the presence in the Pennsylvanian and earliest Permian of Europe of typical embolomeres, long-snouted fish-eaters with characteristic cranial structures.

We now note the evidence that this same group was abundantly represented at this time in North America.

Best known of American genera is that abundant in the Lower Permian of Texas, usually but incorrectly termed *Cricotus*; this name belongs to a poorly known Pennsylvanian genus, but the term *Archeria*, applied to a humerus of the Texas form, is available. Three species have been described; in order of priority they are *"C." crassidiscus*, *"C." hypantricus* and *Archeria robinsoni*. The types of all three are from nearly the same horizon and no adequate morphological distinctions are known.

Fragmentary remains of *Archeria* are not uncommon in various Wichita formations in the Texas redbeds, from the Pueblo upward to the Belle Plains, and have recently been discovered in the Clyde as well. There are, however, no traces of the genus in the Clear Fork group; the end of the Wichita appears to mark the end of the history of the embolomeres.[1] The genus is absent from the New Mexico redbeds.

Published data on *Archeria* are limited. The early literature on the Texas *"Cricotus"* was assembled by Case in 1911 (pp. 72–75, 76–78, 145–148, pl. 24, figs. 1, 2; pl. 25; cf. also Cope and Matthew 1915, pl. 16a). Broom (1913, pp. 567–568, figs. 1–3) has published notes on the skull; Watson (1929, p. 229) has pointed out that a partial braincase described but not identified by Williston (1918, figs. 14c-e) is probably that of *Archeria*. Among the earliest described remains of the Texas genus were two articulated skeletons, but these were unsatisfactory in condition (cf., however, Cope and Matthew 1915, pl. 16a). Apart from these, almost all known material had until recently consisted only of isolated elements, even at the rich Briar Creek bonebed (Case 1915, pp. 157–176, pl. 22 etc.[2]) The writer's long search for *Archeria* remains was finally rewarded by the discovery in 1939 of a number of articulated skeletons in the Geraldine bonebed in the Admiral Formation in Archer County, Texas. This material is at present being prepared. It is hoped that eventually a fairly complete account of the anatomy of this form may be based upon it, but meantime only a few notes are available.

In general proportions, *Archeria* closely resembled *Pteroplax* of the European Pennsylvanian. Like that form, the genus was surely an

[1]Dr. J. W. Stovall informs me that he is describing a large *Archeria*-like jaw from an Oklahoma formation which may be of Clear Fork age.

[2]Case's pl. 22, figs. 6 and 7 are not femora of *"Cricotus,"* but of *Ophiacodon*; the femur is shown in pl. 24, fig. 5.

aquatic fish eater, long-snouted, with a long and slender body and powerful tail, and with small limbs. *Archeria* was of modest size, with an overall length of ½ to 2 meters; skulls have generally an estimated length of but 15 to 20 cm. but one described by Case was about 26 cm. in length.

Except that the snout was rather longer and more slender, the skull roof is closely comparable in every way to that of *Pteroplax*. There is a separate intertemporal, which Broom did not distinguish from the postorbital. The palate is as yet unknown. The braincase is not adequately known except for the occipital elements and basicranial region seen in the Williston specimen noted above. There is a primitive single condyle, and exoccipitals of restricted size do not extend forward of the vagus opening. The basisphenoid is well ossified. The pituitary region and that of the interorbital vein and eye-muscle recess behind it are developed similarly to the condition seen in *Seymouria*. As in the Seymouriamorpha, the so-called sella turcica posterior to this region ends dorsally in an expansion, presumably extended in cartilage, which may be identified as a development in the embryonic pila antotica.

The lower jaw is built as in *Pteroplax*, with the characteristic large meckelian fenestrae. The teeth are numerous, slender, closely crowded and bevelled at their tips.

The vertebrae are adequately known, and have the typical embolomere structure in both presacral and caudal regions. About 40 presacrals are present. The sacral vertebrae appear to be similar to those of *Pteroplax*, but there is a definite sacral rib.

Despite the great resemblance to *Pteroplax* in every other regard, the *Archeria* shoulder girdle shows not the slightest resemblance to the specimen which Watson tentatively associated with that European form; instead, it is built on a normal labyrinthodont pattern. The scapulocoracoid is of normal structure, although with an unusually large supraglenoid foramen (there is but a single center of ossification). The interclavicle is a large flat rhomboidal structure, with the posterior end produced into a short stem. This is overlapped in the usual fashion by expanded triangular clavicular expansions; the dorsal part of the clavicle extends upward at right angles to the ventral expansion as a slender rod. Articulating with this dorsally was a typical amphibian cleithrum, rod-like but with a modest dorsal expansion. There is no evidence of a posttemporal element for connection with the skull, or of any place for its attachment to the cleithrum.

The pelvis is of the typical embolomere type. The limbs were small. The major elements were correctly identified by Case from the Briar Creek material, except that his supposed "*Cricotus*" humerus is that of *Parioxys* or a related genus, and the true humerus is that which he named *Archeria* (1915, pp. 170–171, pl. 23, figs. 7, 8). This is a flattened type of humerus which may be correlated with aquatic habits. A notable feature is the presence of an entepicondylar foramen. This structure is characteristic of reptiles, but almost unknown in amphibians. Its presence in such diverse forms as *Deudrerpeton* and *Diplocaulus* suggests, however, that it may be a primitive tetrapod character. Foot material is present in several instances, but I have not as yet been able to determine the phalangeal formula. There is a well developed ventral armor, but no evidence of other squamation.

Cricotus

This is the typical genus of the Embolomeri of Cope. The name is frequently applied to the Texas embolomere here termed *Archeria*, but the genus was founded upon specimens from an early Stephanian locality near Danville, Illinois, which Cope believed to be of Permian age (Cope 1875a, p. 405; 1877, pp. 185–186; 1884, p. 39; Case 1900, pp. 708–709, figs. 12–15; 1911, pp. 75–76, etc.). The material consisted merely of isolated intercentral and pleurocentral elements. Three species were described, *heteroclitus*, *gibsoni* and *discophorus*, but it is doubtful if more than one can be maintained. Shortly after the discovery of this deposit, true Permian deposits were discovered in Texas. In them were found similar embolomerous vertebrae (Cope 1878, p. 522 etc.). Believing the two deposits to be of the same age, Cope assumed the identity of the forms in the two localities and applied the name *Cricotus* to the Texas material as well. It is, unfortunately, highly improbable that there is any generic identity between the type material and the Texas embolomere of considerably later date. Little can be deduced concerning the position of *Cricotus* among the Embolomeri. The one diagnostic feature of the genus, whereby it can be readily distinguished from the Texas form (or forms), is that given by Cope (1884, p. 28) in a species diagnosis, namely that the dorsal intercentra in the Illinois genus are much narrowed or pinched above. This is also true, as noted above, of *Pteroplax*, the European contemporary of *Cricotus*.

Eobaphetes

This genus, originally described by Moodie (1911) as "*Erpetosuchus*" *kansensis*, is based on a lower jaw and a few other fragments from a Kansas carbonaceous deposit, the exact topographic locality of which is uncertain. It is, however, believed to be from a horizon close to the Cottonwood Limestone and hence equivalent to the lower Wichita of the Texas Permian (Romer 1930, p. 129; 1935, p. 1631). The jaw is that of a typical embolomere, with the characteristic internal fenestrae seen in *Pteroplax* and *Archeria*. But although it is perhaps contemporaneous with the latter genus and from the same land mass in the midcontinental region, the jaw differs markedly in the presence of stout teeth of labyrinthine structure and a well-developed sculpture on the anterior part of the jaw ramus (the skull also is heavily sculptured).

The name is unfortunate, since *Baphetes*, as noted elsewhere, is earlier and probably quite unrelated.

In 1930 I associated the *Eobaphetes* jaw with *Leptophractus* of the Linton, Ohio, Pennsylvanian because of similar sculpturing and marginal teeth and the supposition that the latter genus was likewise an embolomere. These morphological features, however, are feeble guides, and *Leptophractus* proves, to my embarrassment, not to be an embolomere.

Spondylerpeton

(Fig. 12)

A nodule from the famous late Westphalian plant deposit of the Mazon Creek region of Illinois contains the only material ascribed to *Spondylerpeton spinatum* (Moodie 1912, pp. 355–357, pl. 8; pl. 9, fig. 1, etc.; Romer 1930, pp. 132–133, fig. 25). This consists of two caudal vertebrae of an embolomere; the intercentrum (with attached chevron) is a complete disc. The specimen shows the presence of a large embolomere in this Pennsylvanian deposit, but nothing more.

Calligenethlon

(Figs. 12, 44)

The only embolomere skull material as yet surely identified in the American Pennsylvanian is a small specimen, *C. watsoni*, described by Steen (1934, pp. 484–486, figs. 18, 19, 20B, pl. 2, fig. 1) from the

hollow tree material of the Joggins, Nova Scotia. This exhibits the central portion of a skull roof of typical anthracosaurian type, closely comparable to the same region in *Pteroplax* and *Archeria*. The few vertebral centra associated show a typical embolomerous appearance when seen in side view. Steen notes that one centrum when seen in end view is a "nearly complete ring". An incomplete shoulder girdle associated with the skull shows the presence of expanded clavicles, but little else.

With this type may be associated certain other Joggins specimens. As Steen implies (1934, pp. 494–495, fig. 26), it is probable that *Atopotera moneres*, based by her on a partial skull, may be a synonym; its structure may be brought into line with *Calligenethlon* on the assumption that the bone identified as a supratemporal is actually the intertemporal.

On the slab with the rhachitome *Dendryazousa*, but not necessarily associated with that form, are postcranial materials of embolomere type (Steen 1934, pp. 483–484, fig. 17) which may belong to *Calligenethlon*. The vertebrae are similar to those found with the *Calligenethlon* skull. Steen notes that when seen in end view the centra are of two types: one, presumably pleurocentrum, is a complete ring; the other type is incomplete. A pelvis on this slab is in general of embolomere type, although the characteristic dorsal process, which Steen reasonably believes to have been present, is not preserved. This same material includes an incomplete shoulder girdle comparable to that of *Archeria*, with expanded clavicles, and a scapula with a large supraglenoid fossa.

A further embolomerous specimen from the Joggins is an isolated pelvis, typically embolomerous and with the dorsal process preserved.

In the *Calligenethlon* type and the material which may be associated with it, we thus have a form which exhibits most of the characteristic features of the *Pteroplax-Archeria* embolomere group. The remains are those of animals of small size, as would be expected of tree-stump inmates; one may reasonably assume that we are dealing with young individuals of a form which as an adult may have reached much larger proportions.

We may note here, for want of better connections, a fine embolomerous pelvic girdle which was discovered in the Carboniferous mining district at Stellarton, Nova Scotia ("Pictou"), and figured by Watson (1926, pp. 235–236, fig. 27). This is a much larger bone than either of the Joggins specimens, but may well have been borne by an adult of *Calligenethlon* or a related form.

The vertebral structure mentioned above is of phylogenetic interest. If, as here advocated, the ancestral type of labyrinthodont vertebra was essentially rhachitomous in nature, we would expect that in the ancestral embolomeres there would have been a stage in which the centra were incomplete rather than full rings. The condition of incomplete ossification in ring-fashion of one of the two *Calligenethlon* elements — presumably the intercentrum — may well be due to immaturity, but may be reminiscent of a similar stage in the adults of more primitive members of the group.

Pholidogaster

(Figs. 12, 44, 45)

The oldest known labyrinthodont skeleton of any sort, as well as the oldest known embolomere is the type of *Pholidogaster pisciformis*, from the Gilmerton Ironstone of the Upper Mississippian (Lower Namurian) of the Edinburgh coal field. Of all known labyrinthodonts, only the Greenland ichthyostegids (in which the postcranial skeleton is unknown) are older, and the oldest known loxommid is a contemporary. *Pholidogaster* is important, therefore, in the attempt to interpret the early evolution of the labyrinthodont skeleton. The type was figured by Huxley (1862); Watson (1929, pp. 230–233, figs. 7–11) has redescribed this specimen and reasonably associated with it a skull from the same locality.

The skeleton, as preserved, measures about a meter in length, this including a fair portion of the tail. As Watson notes, the specimen is disappointing in that little detail can be made out in most regions.

In the type, the skull (with a length of about 18 cm.) is exposed from the ventral surface; little can be seen except the general outlines and the outer surface of the jaws which partially cover it. The jaws do not decrease in depth anteriorly as markedly as in later embolomeres. The second skull associated by Watson shows, however, much of the roof and palate. The skull is moderately long in proportion to its width, with a broadly rounded snout and orbits placed just back of the middle of the skull length; these are seemingly primitive proportions, rather in contrast with those of later typical embolomeres. As in later forms, cheek and table were but loosely connected; there were small tabular horns. Few of the sutures of the skull roof can be made out, but those of the table show the characteristic anthracosaur pattern, and the intertemporal pushes far forward toward the orbit as in *Pteroplax* and *Archeria*. The palate

is in general of the primitive and anthracosauroid type seen in later embolomeres, with movable basal articulation and narrow vomers between internal nares placed far forward. The vomer does not exhibit teeth. There is a pair of large tusks on the palatine, but the dentition departs from the common primitive pattern in the presence of a pair of smaller teeth behind the main palatine tusks and of a row of three pairs of ectopterygoid teeth. There is a deep flange, as in *Palaeogyrinus*, on the pterygoids.

Postcranially, trunk and tail are long and slender, as in later embolomeres. There is a typical ventral squamation. Little can be seen of the trunk vertebrae, but Watson notes that in favorable cases a typical embolomerous condition can be made out. The tail vertebrae, however, show a semi-rhachitomous condition, perhaps primitive. The intercentra are ventral wedges; the pleurocentra simulate, in lateral view, the rhachitomous type, but Watson believes that they may form a complete ring, or at least a nearly complete ring formed of two closely apposed hemicylinders.

The limbs are small and weak; Watson has described such details as can be made out. The dermal shoulder elements are expanded ventrally in a fashion similar to that of *Archeria*. There is a well-ossified puboischiadic plate. The ilium has a rod-like posterior process; whether or not it has a dorsal expansion is not clear.

Pholidogaster, from its elongate shape and feeble limbs, appears to have been an aquatic fish-eater like the later typical embolomeres. Apart from the question of vertebral construction, it might well be close to the ancestry of the seymouriamorphs as well.

I may note here the presence, in the late Mississippian of West Virginia (Hinton Shales, Mauch Chunk Group), of an embolomere, as yet undescribed, which shows a dermal girdle and possibly other features similar to that of its European contemporary (Romer 1941a).

Palaeogyrinus

(Figs. 4, 5–8, 44, 45)

The oldest amphibian skull of which a reasonably complete account is as yet available is that of the unique type of *P. decorus* (Watson 1926, pp. 215–222, figs. 12–17) from the early Pennsylvanian (Lanarkian-Namurian) of Pirnie, Fifeshire (Scotland). No jaw nor postcranial material of any sort is associated, but there are numerous features which indicate that it is an anthracosaur and may be, as Watson believes, an early embolomere.

The skull roof shows the typical anthracosaur construction of the table and its loose attachment to the cheek. However there are differences from the characteristic genera of the later Pennsylvanian in the shorter and more rounded snout, and in the greater posterior extension of the postfrontal, so that the intertemporal does not approach the orbital margin. Grooves are present for much of the lateral line system; the nares, as restored, are much farther apart than in typical embolomeres; the maxilla is unusually short.

The anterior portion of the palate is, unfortunately, unknown; the posterior part of the palatal aspect of the skull is primitive in construction, and deep pterygoid flanges (alongside elongate basitemporal fenestrae) indicate that the jaw was deep posteriorly. The epipterygoid was ossified, although the portion present consists of little but the columella cranii, and took part in the basal articulation.

The braincase is well preserved. It agrees in significant diagnostic features with that of *Pteroplax*, and hence may be considered as representative of embolomere construction.

The occipital condyle is, as in primitive temnospondyls, a single circular concave structure formed by the very well-ossified basioccipitals and exoccipitals. The latter element is, in contrast to typical temnospondyls, restricted in area; it does not extend forward of the vagus opening, and is sharply separated from the opisthotic laterally and the supraoccipital region dorsally; in this the exoccipital is in agreement with that of seymouriamorphs and reptiles. No opening for a hypoglossal nerve is apparent. The supraoccipital region is well ossified, and not by any extension from the exoccipitals. This leads to a belief that a distinct supraoccipital ossification was present, although there is no visible suture separating this area from the otic bones. The posttemporal fossae were small or absent — an unusual feature in amphibians, but apparently confirmed for embolomeres by a similar construction in *Anthracosaurus*.

The otic elements are well ossified and, as in seymouriamorphs, appear to be separated by a distinct suture passing through the region of the fenestra ovalis. This last structure, Watson notes, is extraordinary in that it is not a developed fenestra, but merely a depression in the surface of the bone, seemingly representing a transition from the fish condition — a pseudo-fenestra ovalis.

In contrast with the temnospondyls, in which the lateral wall of the braincase appears to have continued forward without interruption, in bone or in cartilage, from the otic region to the sphenethmoid, the lateral wall here is interrupted by a large vacuity, with well-defined

outlines somewhat in the fashion of seymouriamorphs and reptiles. Ventral to this, a bar of bone extends forward from the "sella turcica" to the sphenethmoid above a second opening — presumably that for the interorbital vein and the place of origin of eye muscles. *Palaeogyrinus* is here better developed than *Areheria*, in which this bar appears to have been unossified; *Pteroplax*, however, shows the *Palaeogyrinus* construction.

The basisphenoid is well ossified. The basipterygoid processes agree with those of seymouriamorphs and reptiles rather than those of temnospondyls in that they are turned sharply downward and in that the articular surfaces face more anteriorly than laterally. The sphenethmoid is well ossified and relatively high and narrow.

There is no evidence that *Palaeogyrinus* is technically an embolomere. It is, however, a very primitive amphibian, definitely an anthracosaurian, and one which may well be a structural ancestor of the embolomeres if not actually a member of that group.

Anthracosaurus

(Fig. 45)

This generic name is often applied to a variety of British Carboniferous labyrinthodonts, but, as Watson notes (1929, pp. 225–227, figs. 3, 4, pl. 3), the only known specimen is the type of *A. russelli* described by Huxley (1863, pp. 56–68, figs. 1, 2). This is a skull from the early Pennsylvanian (Lanarkian) Black Band Ironstone of Airdrie, Scotland. *Anthraeosaurus* was a large amphibian; the overall length of the skull is about 40 cm.

Unfortunately the dorsal surface is concealed, and, while palate and occiput are exposed, the preservation is poor and little detail can be made out. That the form is a proper member of the Anthracosauria, to which group it gives a name, seems certain from the palatal structure, with the nares rather close together and the vomers consequently narrow. The palate is of the primitive closed type, with slender parasphenoidal rostrum and movable basal articulation. The vomer is toothless; on the other hand, two tusk-pairs are present on the ectopterygoids. The anterior marginal teeth are massive. Noteworthy is the position of the suspensorial region, unusually far back of the skull table.

The condyle was a single structure, in primitive fashion. The tabular is massively built, with a powerful "horn". There is (as in *Palaeogyrinus*) little evidence of the presence of posttemporal fossae.

Crassigyrinus

(Figs. 14, 45)

The only specimen of *C. scoticus* (Watson 1929, pp. 233–234, fig. 12) consists of the right side of a large skull from the Carboniferous of the Midlothian region of Scotland; the matrix suggests that it is from the Lower Namurian Gilmerton Ironstone and hence one of the oldest known labyrinthodonts. In default of any knowledge of the skull table or palate, it is difficult to be certain that the specimen is an anthracosaur at all; however, the fact that the cheek was detached from the skull table along the line of weakness present in embolomeres is suggestive. The snout lacks the elongation and slimness seen in the typical late Carboniferous embolomeres, and Watson notes other peculiarities such as the very great length of the suspensorium; the large external naris; and the broad cheek, with the orbit far medially and the maxilla passing back so as to underlie part of the quadratojugal and thus exclude the broad jugal from the margin of the jaw.

The length of the suspensorium is reminiscent of *Anthracosaurus*. Unfortunately there is no basis of comparison between the *Anthracosaurus* palate and the *Crassigyrinus* skull roof. It is not impossible that, despite some difference in age — *Anthracosaurus* is somewhat later — the two may be related. They are the largest known anthracosaurs.

As Watson notes(1929, p. 234), it is possible — but not capable of proof— that the Gilmerton jaw fragment named "*Macromerium*" *scoticum* by Lydekker (1890, p. 162) belongs to this form. It is also possible that a large dermal shoulder girdle from Gilmerton which Huxley (1862, pl. 11, fig. 12) assigned, but without proof of association, to *Loxomma*, belongs here. The moderately expanded ventral plates are only weakly sculptured, in contrast to the girdle of *Pholidogaster*, found in that deposit. The specimen is of interest as exhibiting an incipient, short and blunt, clavicular stem, a feature highly developed in the Seymouriamorpha and reptiles.

Papposaurus

Watson (1914) described as *P. traquairi* a femur from the Lonehead Ironstone of the Scottish Mississippian. Its describer believed it to be reptilian in type, but, as White (1939, p. 383) has noted, the

bone is quite similar to that of the embolomere *Archeria*, and presumably pertains to one of the embolomeres of the Scottish Mississippian, *Crassigyrinus* or *Pholidogaster*.

Eosaurus

Marsh in 1862 described two large disc-shaped structures from the Nova Scotia Joggins as *Eosaurus acadianus*. These are from a different and higher horizon than that of the famous erect trees, and are presumably Westphalian in age. Marsh believed them to be centra of an "enaliosaurian", i.e., an ichthyosaur (or plesiosaur). This is impossible. They may be embolomerous, although they do not conform in detail to the centra of known embolomeres.

DISCUSSION

Above we have considered a series of amphibians which appear to have constituted a considerable proportion of the fauna of larger tetrapods of the Carboniferous but became extinct at the beginning of the Permian. Except that the loxommids are excluded, for reasons earlier discussed, these constitute the Embolomeri as treated by Watson. As that writer clearly pointed out, they show numerous primitive features and in addition are highly suggestive of relationship to the ancestry of reptiles. The pro-reptilian characters and many of the primitive features as well are shared by the embolomeres with *Seymouria* and its allies, and these two groups are here considered as suborders forming the Order Anthracosauria.

Primitive features shared with early temnospondyls are numerous. The long lacrimal, which may extend from orbit to naris, and the presence of an intertemporal are primitive features of the skull roof. In the palate, the closed condition of the interpterygoid vacuities and the movable condition of the basal articulation are common primitive features. In the braincase we may note the general high degree of ossification and the single occipital condyle in which the basioccipital plays a prominent part. These primitive characters persist in embolomeres (and seymouriamorphs) to the end of their history, whereas they are generally abandoned by temnospondyls at an early date.

There are, however, numerous features which the embolomeres share with the Seymouriamorpha but which are not found in temno-

spondyls; these are the definitive characteristics of the Anthracosauria. We may note particularly in the cranial region: the large tabular, articulating with the parietal; the narrow vomers; the choanae relatively close together and anteriorly placed; the fenestration of the braincase between otic capsule and sphenethmoid; widely open interorbital vein foramen; basipterygoid processes turned downward and forward; general absence of vomerine and symphysial dentary tusks; exoccipitals not extending upward to the skull roof; and apparent tendency for development of a separate supraoccipital. Postcranially both embolomeres and seymouriamorphans show, in strong contrast to temnospondyls, pleurocentra that have developed into stout ring-shaped true centra which form the main elements in the column. There are very probably other features of the postcranial skeleton which may be common to embolomeres and seymouriamorphs, but our imperfect knowledge of the structure of the former limits us here. For example, *Archeria* has an entepicondylar foramen in the humerus, as does *Seymouria*, but we do not know the humerus in any other embolomere; it is possible that the embolomeres had a 5-toed manus, but the point is not proved; both show at least a tendency toward development of a stem to the interclavicle, but this structure is not well developed in any known embolomere.

The later, typical embolomeres and the seymouriamorphs differ in a number of features, discussed in connection with the latter group, which serve to give a differential diagnosis of the two suborders. With one or two exceptions these features are such as show a closer approximation of the seymouriamorphs to the reptiles, and certain of them are probably non-primitive characteristics acquired by an early stock common to these two groups after divergence from a common early anthracosaur ancestry. For the most part one may easily consider this common ancestor to have been an embolomere.

The problem of the primitive construction of vertebral centra, however, is a more serious one. We have here assumed that the ancestral labyrinthodont was essentially a rhachitomous form, with a crescentic intercentrum, forming a partial ring but incomplete dorsally, and the pleurocentra appearing as paired lateral wedges. In both embolomeres and seymouriamorphs the pleurocentrum has become the major element — the "true" centrum — as a complete cylinder. In the typical embolomere the intercentrum has likewise become a complete disc; in the seymouriamorphs it is an incomplete crescent, as in the presumed ancestors. Unless we assume, unnecessarily, that the intercentrum had reversed its evolutionary trend

in seymouriamorph evolution, and had become a disc only to undergo secondary reduction to a crescent again, we must assume a stage in embolomere ancestry where the vertebral central structure was that of the seymouriamorphs. That that is the case is suggested by several facts: (1) even in *Archeria*, where the intercentra are perfect discs, they are notably thinner than the pleurocentra; (2) in *Pteroplax*, although the intercentra are complete, they are barely complete, thin above and rather wedge-shaped; (3) in *Calligenethlon* and in *Diplovertebron* — here treated as a seymouriamorph but seemingly intermediate in nature — the intercentra are not quite complete dorsally; and the evidence for the early and primitive *Pholidogaster* is none too satisfactory.

It is thus probable that the ancestral embolomeres lacked the characteristic intercentral disc which is a diagnostic feature of the later members of the group. It does not, however, seem necessary — particularly in our present state of imperfect knowledge — to separate in any marked fashion the earlier and later types.

The typical embolomeres of the *Pteroplax-Archeria* type are apparently characteristic of the Middle and Upper Pennsylvanian and lowest Permian. These were very probably a close-knit group of somewhat specialized, long-snouted fish eaters. *Pholidogaster* is quite possibly an ancestral form. But in the earliest Pennsylvanian of Great Britain we find a number of incompletely known genera, in which the long-snouted skull shape was not developed. These may well represent a primitive embolomere stock from which typical embolomeres, seymouriamorphs and reptiles may have been derived. But their vertebral structure — and, indeed, their entire postcranial anatomy — is quite unknown.

SEYMOURIAMORPHS

Seymouria of the American Permian is a primitive tetrapod structurally close to the boundary between amphibians and reptiles and often included in the latter class. This genus and seemingly related types — *Rhinosaurus, Kotlassia, Lanthanosuchus, Discosauriscus* and *Phaiherpeton* of the Permian, and *Diplovertebron* of the late Pennsylvanian — are here, however, considered as forming a group of anthracosauroid labyrinthodonts. Also discussed here, as seymouriamorphs or cotylosaurs, are several problematical genera of the late Pennsylvanian — *Solenodonsaurus, Tuditanus, Eusauropleura* and *Adenoderma.*

Seymouria

(Figs. 4–9; 12, 14, 47)

This famous genus was first described by Broili (1904, pp. 80–84, pl. 13, figs. 1–3) as *S. baylorensis* mainly on the basis of skull material. Later descriptions include an account by Williston (1911, pp. 48–67; 1911a) of a complete skeleton, and a thorough discussion of structure and affinities by Watson (1919a; see also Broom 1922, pp. 457–458, fig. 7; Romer 1928, etc.). A comprehensive account of the anatomy has been recently given by White (1939), based on the skeletons of a considerable number of individuals which had been collected more than half a century before but had long lain neglected in museum drawers. All the earlier discovered remains of *Seymouria* were obtained from the upper, Clear Fork, beds of the Texas Permian; recently, however, characteristic materials have been discovered in the Belle Plains, Admiral and Putnam formations of the Wichita group. As noted by several writers, *Conodectes favosus* (Cope 1896; 1896a, pp. 129–130,) is probably generically identical and has priority. White, on rather feeble bases, has diagnosed *Conodectes* as a separate genus with the laudable purpose, I suspect, of preventing the race of "priority-chasers" from replacing the familiar *Seymouria* with an obscure name based on a battered skull fragment, never figured and impossible to identify from the original description.

Seymouria was a tetrapod of modest size and stocky build. Skull lengths average about 100–130 mm.; the length to the pelvis is about 37–40 cm.

The skull was rather low as compared with that of early reptiles, rather high as compared with that of contemporary temnospondyls; the cheek descends sharply from the broad flat skull table; cheek and table are firmly united anteriorly. In contrast with typical embolomeres, the snout was short and broadly rounded; the orbits are about midway of the length of the skull. The otic notch is highly developed, extending far forward toward the orbit and deeply excising the squamosal. The dermal roof is deeply sculptured in amphibian fashion, and, as White notes, there are apparently faint traces of lateral line grooves. In one instance sclerotic plates, about 20 in number, were found in the orbit.

The roofing pattern is that of a typical and rather primitive anthracosaur. The tabular is in broad contact with the parietal. As in amphibians, but not in typical reptiles, the postparietals are paired

and broadly developed on the dorsal surface of the roof. The lacrimal, perforated by a canal for the lacrimal duct, extends from the orbit to the narial region, where there is a superficially developed septomaxilla; the external nares are close to each other.

The palate is of primitive anthracosaurian pattern. The vomers are narrow; the elongate choanae are far anterior in position. There are broad and well developed pterygoid flanges. The two pterygoids meet broadly anteriorly; the interpterygoid vacuities are practically non-existent, the pterygoids being closely apposed to the cultriform process of the parasphenoid. Posteriorly the parasphenoid spreads far laterally to the margin of the fenestra ovalis, and, more medially, forms a pair of "basisphenoidal" tubera. It does not extend far posteriorly and in consequence the basioccipital is well exposed. The parasphenoid has a V-shaped posterior margin repeated in certain other anthracosaurs. There is a movable basal articulation. The well-developed basipterygoid process is received into a socket in the pterygoid. The epipterygoid, which commonly takes part in this articulation, has been reported only in the large skull fragment which is the type of *Conodectes*, and even there appears to have been poorly ossified. There is a prominent descending flange of the squamosal which broadly overlaps antero-laterally the quadrate ramus of the pterygoid. The quadrate extends far forward along the lateral surface of the pterygoid, and a groove extending forward from its termination suggests a cartilaginous continuation of the palatoquadrate beyond this point. The articular surface of the quadrate is more prominently bilobed than is usual in amphibians.

The marginal teeth are stout and labyrinthine in structure (Broili 1927b). On the palate, tusk pairs are present on the vomer and palatine, but the ectopterygoid is toothless. The palatal ramus of the pterygoid is covered by shagreen teeth, as are much of the palatine and ectopterygoid.

The occipital condyle is single. The basioccipital is highly developed and runs forward ventrally to meet the basisphenoid. The exoccipital, containing a hypoglossal foramen, is relatively small and, as in embolomeres and reptiles but in contrast with many temnospondyls, does not extend forward of the vagus foramen nor far upward toward the skull roof. The supraoccipital region is unossified in the typical *Seymouria* material; there is a small ossification in the *Conodectes* type, but there was in any case a large supraoccipital cartilage which was nearly completely covered posteriorly by descending flanges of the postparietals and tabulars. The tabular flange

nearly covers the entrance of the posttemporal fossa. A descending process of the tabular forms the lateral margin of the fossa; this presumably included an endochondral component. The curved, unfinished tip of this process was apposed to a similar surface on the conjoined prootic and opisthotic. White suggests that this area was penetrated by the upper end of the hyoid, but it is reasonable to assume that the lateral wall of the fossa was completed here by intervening cartilage.

Both opisthotic and prootic are thoroughly ossified and are suturally distinct. The latter element extends far posteriorly medial to the supratemporal fenestra; seemingly it supplants the supraoccipital to some degree. The fenestra ovalis is placed far laterally, at the tip of a rather tubular extension of the pair of otic elements. Openings for both palatine and main rami of the facial nerve are present on the outer surface of the prootic. The upper margin of the prootic slopes downward anteriorly, as in primitive reptiles, leaving a wide unossified gap; the orbital plate, or laterosphenoid, present in temnospondyls, is absent.

The basisphenoid is well ossified as a purely ventral structure. As in primitive reptiles, its posterior margin forms internally a broad transverse ridge, often termed the dorsum sellae, with a median forwardly projecting spur. In front of this point the primitive transverse canal, open above, is broadly excavated for eye muscle origins. Still farther anteriorly is a depression in the floor of the braincase in which lie the internal openings of the carotid arteries, which entered the bone posterior to the basipterygoid processes.

Anterior to the basisphenoid, but distinct from it, is the sphenethmoid; it is widely separated posteriorly from the otic complex, leaving much of the lateral wall of the brain cavity unossified. The interior of the sphenethmoid is unossified; its ossified walls form a V, rising on each side to the skull roof, but unenclosed above except by the dermal bones. White believes that separate basal (presphenoid) and lateral (orbitosphenoid) components are present.

The lower jaw is of normal labyrinthodont construction. The coronoids bear a shagreen of teeth; the splenial is broadly exposed on the inner surface. There is no retroarticular process.

The ossified stapes consists of a short slender rod, presumably representing part of the shaft only. It will be noted that the production laterally of the region of the fenestra ovalis greatly reduces the necessary length of the stapes.

There were 23 or 24 presacral vertebrae, a single major sacral vertebra (with, however, the next segment serving an accessory sacral function), and a tail of considerable length — presumably with 40 vertebrae or more.

The vertebrae are, as all describers have agreed, exceedingly similar to those of cotylosaurian reptiles, particularly in the presence in the trunk region of characteristically "swollen" neural arches. These are strongly convex in end view, with zygapophyses facing directly dorsally and ventrally, far out from the mid-line; neural spines are little developed. In the anterior cervicals and the caudals the arches are narrower, and the spines better developed. The atlas-axis complex shows essentially a persistent rhachitomous structure, but the central structure in the remainder of the column is close to the reptilian plan. The pleurocentra are, as in the embolomeres, true, complete centra of amniote type, centered directly under and fused with the neural arches in the trunk vertebrae. The intercentra are ventral crescents and as ossified are relatively small, both in antero-posterior measurement and in dorsal extension; however a gap above the ossified intercentra indicates a cartilaginous extension far toward the top of the central region. In the tail, the neural arch tends to be centered at a more anterior position than the centrum, so that the suture between the two is tilted at a considerable angle. With decreasing height of the true centrum the arch comes close to the intercentrum or in contact with it, thus simulating superficially the embolomerous vertebral topography.

The ribs are distinctly double-headed throughout; in the cervical and caudal regions tuberculum as well as capitulum are distinct processes; in the dorsal region the tubercle is merely a projecting articular facet. The tubercular articulation is, throughout, with a projecting diapophysis, the capitular attachment is with the intercentrum except for the sacral and postsacral series, where the head attaches to the anterior part of the centrum. The subscapular ribs are expanded distally, but without evidence of uncinate processes.

The dermal shoulder girdle includes a short splint-like cleithrum, a clavicle expanded ventrally to a moderately high degree and an interclavicle which bears a long rod-like posterior extension. This last feature is, as we have seen, most unusual amongst amphibians and is a typically reptilian structure. The ventral plates of the girdle are but lightly sculptured. The scapulo-coracoid is again reptile-like in the presence of a distinct coracoidal ossification occupying the ventral portion of the girdle below the level of the glenoid

fossa. The supraglenoid foramen is relatively small; no glenoid foramen was discovered, although a nutrient foramen is present in this area.

In the pelvic girdle pubis and ischium are both well ossified and roughly comparable to these structures in both embolomeres and primitive reptiles. The posterior process of the ilium is not greatly elongate, and there is a marked dorsal expansion to which there is attached internally the broad sacral rib. The iliac blade, however, has not attained the typical reptilian condition (cf. Romer 1922, pp. 559–560; Romer and Price 1940, pp. 126–127, etc.) The articular surfaces of the limb bones are incompletely ossified. The humerus is a short but very stout structure, with highly developed muscular processes, and a sharply "twisted" shaft quite unlike that of *Archeria* and resembling more closely that of certain cotylosaurs. An entepicondylar foramen is present. The femur, with a highly developed system of trochanters and a V-shaped proximal ventral ridge, is not closely comparable with that of other amphibian types and greatly resembles that of the primitive reptile *Limnoscelis*. Carpus and tarsus are incompletely known, but do not appear to have been markedly reptilian in nature; there appears to have been lacking the characteristic reptilian specialization in the tarsus, with its loss of tibiale and high development of astragalus and calcaneum. The feet, on the other hand, show a reptilian pattern, with five digits in the manus as well as the pes, and phalangeal formulae of 2.3.4.5.3 (4). The terminal phalanges are flattened, as in certain primitive reptiles as well as amphibians.

There is no evidence of dermal armor or scales.

Rhinosaurus

(Fig. 46)

Fischer de Waldheim in 1847 (pp. 363–366, pl. 5) described, as *R. jasykovii*, a small skull from the former Russian Government of Simbirsk (now Ulianowsk). As far as I am aware there has been no further description or discussion of this form by any later writer interested in amphibians except for early references by Huxley (1859, p. 646) and Owen (1876) and it is not mentioned in Efremov's recent (1940a) list of Russian amphibians; the reasons being, presumably, (1) that it was assumed to be a reptile, and (2) that it is stated to come from the Jurassic oölites of that region. However,

it is clearly not a reptile, but a labyrinthodont; and quite surely it stems not from the oölites, but from the Permian, Zones I-II of which are extensively exposed near the northern limits of the former Simbirsk government.

Rhinosaurus was compared by Huxley and Owen with *Micropholis* because of comparable skull proportions and the presence in both forms of a well developed otic notch. If, however, the skull roof pattern be examined (no other features except the lateral view of skull and jaw are figured or described), it will be seen that *Rhinosaurus* is actually a seymouriamorphan, and one very similar to *Seymouria* itself. Both intertemporal (large) and supratemporal are present.

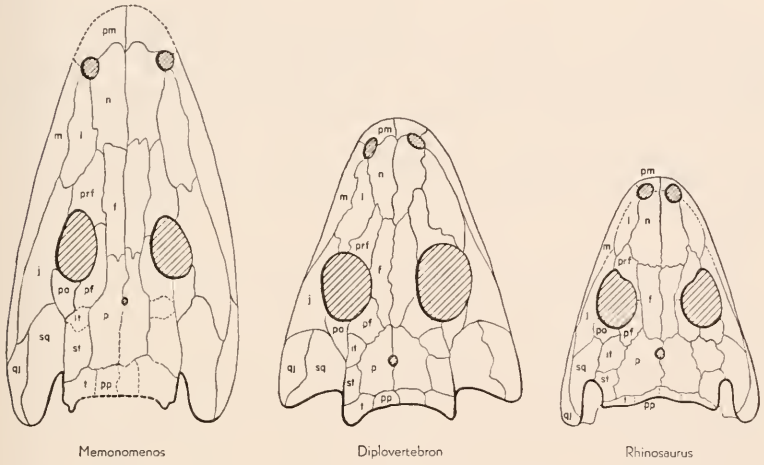

Fig. 46. Skull roofs of anthracosaurs. *Memonomenos* after Steen; *Diplovertebron* after Jaekel; *Rhinosaurus* after Fischer de Waldheim.

The tabulars and postparietals are greatly reduced in extent (the sutures between them are not apparent) and the tabulars are obviously in contact with the parietals — a good key character for the anthracosaurs. As in typical seymouriamorphs, the otic notch is well-developed, and with rounded contours. Also anthracosaurian in nature is the close approximation of the two external nares. The resemblance to *Seymouria* extends even to the notch developed at the anterior end of the orbit. Differences from *Seymouria* are few. The facial region is somewhat more pointed; the lacrimal just fails to reach the orbit; and the otic notch does not extend forward as

far into the squamosal. *Rhinosaurus* is obviously closely related to the slightly earlier American genus.

Lanthanosuchus

L. qualeni is listed by Efremov (1940a, p. 377) as a new seymouriamorph from zone II of the Russian Permian, but is not described.

Kotlassia

(Figs. 4, 9, 12, 14, 47)

This genus is known from a number of specimens from the North Dvina deposits of Zone IV of the late Permian of Russia. It was first described by Amalitsky (1921); Sushkin (1925, 1927, 1928) and Hartmann-Weinberg (1935) gave further data, and Bystrow (1944) has recently published a definitive account of the material. Two species and even a second genus, *Karpinskiosaurus* have been described but all specimens appear to be but variants of a single species, *K. prima*. Except for portions of the limbs, nearly the complete skeleton is known.

It is generally agreed that the genus is related to *Seymouria* (Amalitsky even regarded *Kotlassia* as a subgenus of that earlier form); and most of the structural features are comparable to those seen in that genus. The skull is of the general *Seymouria* pattern, but the face is much shorter and the skull is relatively flat, as in moderately advanced temnospondyls. Skull table and cheek are firmly united anterior to the prominent otic notch. The teeth show a simple labyrinthine structure. The internal nares lack the elongation seen in *Seymouria*. The vomers are relatively broad and are toothless. The palatal teeth are much modified to form a uniform row along palatine and ectopterygoid, in a fashion somewhat comparable to that seen in more advanced temnospondyls. There are definitely developed interpterygoid vacuities, but they are persistently small. The parasphenoid lacks the lateral extension to the fenestra ovalis seen in *Seymouria*, and the "basisphenoidal tubera" are formed from the prootic, lacking the customary parasphenoidal folds.

As in *Seymouria* the basal articulation remains movable and the occipital condyle single. In the occipital flange of dermal bones the postparietal plays a more prominent part than the tabular; the latter does not overhang the opening of the posttemporal fossa as

in *Seymouria*, and the unossified gap seen in *Seymouria* between tabular and otic elements is not present here. The hypoglossal nerve appears to have been postcranial in position, and there is no evidence of a supraoccipital ossification. The otic, basisphenoid and sphenethmoidal segments are built on the same general plan in *Kotlassia* as in *Seymouria*; there are, however, differences in detail. The *Kotlassia* fenestra ovalis is smaller. In both there is a great gap between sphenethmoid and otic capsule along the lateral border of the braincase, but the anterior face of the otic wall is more vertical (and less reptilian) in *Kotlassia*. The basisphenoid is built similarly to that of *Seymouria* but less extensively ossified. On the other hand the *Kotlassia* sphenethmoid is solidly ossified and traversed by the usual pair of olfactory nerve channels.

In the lower jaw the coronoids are toothless; the prearticular extends far forward internally and the surangular externally. The stapes is better ossified than in *Seymouria*, the ossification including part of the footplate, which is pierced by the usual foramen.

Vertebral structure is essentially similar to that of *Seymouria*, but the centra are not as tall and the zygapophyses not as widely separated, while on the other hand the neural spines are better developed. The intercentra are small, but a considerable dorsal extension in cartilage is indicated by the gaps existing between successive centra. A specialization is the fact that in most of the column the intercentra are fused to the centra. There are 26 presacral vertebrae and in general a single sacral vertebra, although exceptionally the sacral function may be divided between two segments.

The interclavicle is of the stemmed type, but the proximal half of the stem is distinctly wider than the distal half (cf. *Phaiherpeton*). The endochondral shoulder girdle is incompletely ossified, and known material shows but a single ossification — that of the scapula. The pelvis is well ossified and in general comparable to that of *Seymouria*. The limbs are relatively small, slender and featureless and are incompletely preserved. There is no evidence of scales, but there were several rows of small sculptured dermal armor plates along the back.

There is no reason to doubt that *Kotlassia*, despite its late Permian age, is a surviving seymouriamorphan. As has been seen it differs in various points from *Seymouria*. Many of these points are of little importance other than furnishing diagnostic generic characters; the basic pattern is essentially the same. We may note, however, that *Kotlassia* shows a number of features indicative of degeneracy or neoteny, such as relatively feeble endochondral ossification in skull

and postcranial skeleton, short low skull, etc. These developments show a parallelism with the later temnospondyls, which strongly suggests that the seymouriamorphs were, from an embryological point of view, not amniote reptiles, but forms which had retained an amphibian style of development.

PHAIHERPETON gen. nov.

(Fig. 47)

Under this new generic term may be noted a series of small forms from the early Permian of central Europe which are apparently seymouriamorphans. They are usually but incorrectly placed in the genus *Melanerpeton*. The list of described forms which belong in this category includes *Archegosaurus austriacus*, *Branchiosaurus moravicus*, *Discosaurus moravicus*, *Melanerpeton falax*, *M. perneri*, *M. longicaudatum*, *M. magnum*, *M. potamites*, *M. pulcherrimum*. All of these forms have been reported from the "Boskovice furrow," a strip of territory running roughly north and south in western Moravia (see Augusta 1936b, pp. 9–12 etc.); localities include: Malá Lhota (near Černá Hora), Trávník, Boskovice, Bačov, Míchov, and Drválovice. The last species listed is known from a single specimen found at Ruprechtice (Ruppersdorf) near Broumov (Braunau), in a Permian basin farther north in easternmost Bohemia, and another single specimen from the Niederhässlich Permian locality in Saxony. A further specimen of *Phaiherpeton* is reported from Horní Kulná, near Kunčice in northeastern Bohemia. The pertinent literature, excluding certain papers of minor importance in Czech, is: Makovsky 1876; Fritsch 1901, vol. 1, pp. 82–83, 96–106, pls. 7, 13–16; Credner 1885, pp. 694–706, pl. 27, figs. 1, 5 only; Stehlik 1924; Augusta 1925, 1935, 1936, 1936a, 1936b, 1937; Steen 1938, pp. 256–259, figs. 38–41.

All the material consists of individuals of small size, a feature which, together with skull shape, has been responsible for their usual assignment to the "branchiosaurs." Recorded lengths of skeletons (usually including the base of the tail) are from 4 to 27 cm., skulls from about 1 to 4.5 cm.

The skulls show considerable variety in proportions, which may be in part (but not entirely) due to differences in age and nature of preservation. All are short and broad (the breadth exaggerated by crushing), with a short suspensorium and extended skull table — "branchiosaur" characteristics obviously related to immaturity and

perhaps neoteny. As Steen has pointed out, the arrangement of elements in the roof is of a normal anthracosaur type; there is always an intertemporal and the tabular is large and in contact with the parietal; the tabular in almost all cases is seen to bear a characteristic "tab" or horn. Unfortunately almost nothing is known of the palate, braincase or lower jaw. The marginal teeth are labyrinthine.

In the vertebral column the number of presacral vertebrae is on the order of 23 or 24; there was a single sacral vertebra and presumably a long tail. Centra have never been described and appear to have been in general unossified.[1] The neural arches, however, are well preserved, and have been observed in both lateral and dorsal views (see, for example, Fritsch 1901, vol. 1, pl. 14; Steen 1938, fig. 40). In many specimens the two halves of the arch are still unfused. There was little spine development; the arches were low, rounded, broad and with the zygapophyses widely separated; they appear, in fact, to be typically seymouriamorphan. Steen notes further the presence of accessory zygapophysial structures, seemingly similar to the hyposphene-hypantrum system of diadectid cotylosaurs, which have a comparable vertebral construction. The ribs are broad proximally and are sometimes seen to exhibit a distinctly two-headed condition. There was a single much expanded sacral.

The dermal shoulder girdle shows a typical seymouriamorph condition, particularly in the long-stemmed interclavicle. A diagnostic feature is the fact that the proximal end of the stem swells out to a distinctly greater breadth than that of the distal end (cf. *Kotlassia*, *Diplovertebron*). There is a splint-like cleithrum. All three pelvic elements are ossified, and the ilium appears to have been rather reptile-like, relatively short and with an expanded blade. The limb elements are short but very stoutly built, as in *Seymouria*; little diagnostic detail can be seen. Manus and pes were both definitely 5-toed in seymouriamorph fashion. The phalangeal formula is incompletely known. In the hand one digit (?the fourth) may have had 5 phalanges; the formula of the pes was perhaps 2.2.3.4.3.

There are few traces of dermal squamation of any sort in most specimens. Augusta (1936a), following its citation by earlier writers, has described a nearly complete set of ventral armor from Černá Hora. He argues that it cannot belong to "*Melanerpeton*" because of the usual absence of evidence of armor in known specimens; an argument, however, that does not have too great validity. He

[1]The "*Melanerpeton*" centra figured by Credner (1885, pl. 27, fig. 4) belong to *Discosauriscus*.

rather arbitrarily assigns the armor to *"Pelosaurus"*, and Kuhn (1933, p. 18) promptly furnished the specific name *augustai*. But it will be noted that the ventral scales show the concentric structure seen in *Discosauriscus*, and that while the armor proper is composed of scales of elongate oval shape, scales at the margin are more nearly circular and close to the appearance seen in that relative of the present genus.

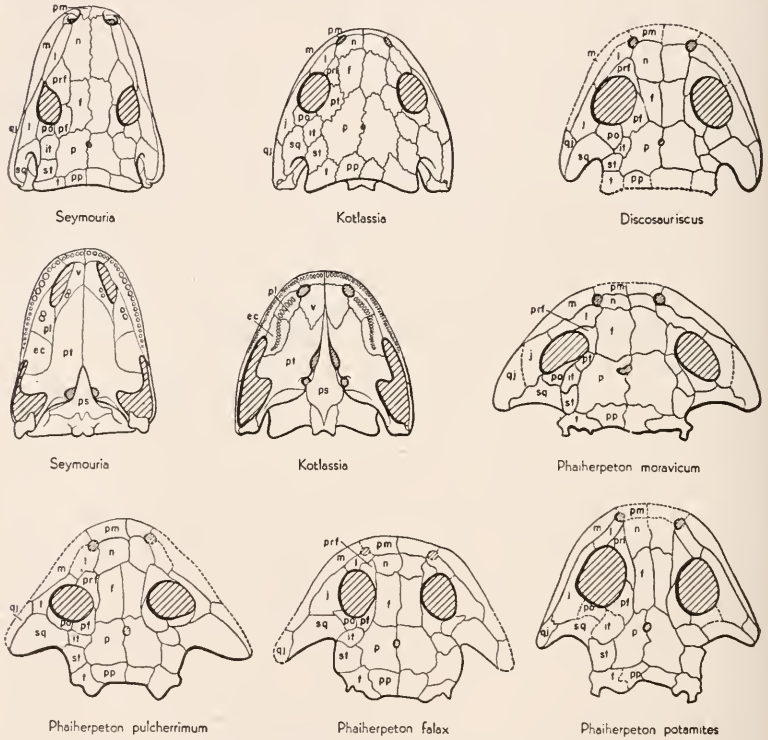

Fig. 47. Seymouriamorphs. *Seymouria* after White; *Kotlassia* after Bystrow; *Discosauriscus* from data in Credner; *Phaiherpeton* after Steen, Fritsch, Credner.

The taxonomy of these forms is a difficult matter. Nine species have been described from the Boskovice beds; it is, to say the least, doubtful whether such a large number of related forms existed essentially contemporaneously in a very restricted area. But although

much of the seeming difference between the various skulls may be due to varied age and types of preservation, it is difficult to include all this material in a single species. As Steen suggests, we may be dealing with a group in an unstable evolutionary stage.

It will be noted that the earliest described species, *austriacus*, has been neglected by all later writers, following Fritsch's statement that it included specimens of two forms, which he described as *Branchiosaurus moravicus* and *Melanerpeton falax*. Obviously the original specific name should be applied to one of the two; and (despite doubts as to the general advisability of this procedure) I herewith designate the holotype of *M. falax* figured by Fritsch (1901, vol. 1, pl. 16, fig. 1) as the neotype of *"Archegosaurus" austriacus*.

Generically, most of these forms have been assigned to *Melanerpeton* and certain of them to *Archegosaurus*, *Branchiosaurus* and *"Discosaurus"*. *"Discosaurus" moravicus* was distinguished from the *Melanerpeton* material of the Boskovice area through the occurrence with the type specimen of small structures similar in appearance to the scales of *"Discosaurus."* Augusta, however (1935), has reasonably interpreted them as inorganic structures and *"D". moravicus* is presumably congeneric with the other material from the Boskovice furrow. The major problem has, however, to do with the true nature of *Melanerpeton*, to which genus this material is customarily assigned. The type of that genus is not any of the familiar members of this group, but *M. pusillum* from Broumov (cf. the discussion under *Chelydosaurus*). This species shows none of the characteristic anthracosaur or seymouriamorph features seen in the material discussed here. The skull proportions differ; there would seem to have been an open, rhachitomous type of palate; there appears to be no intertemporal; there is no proof of the presence of a stemmed interclavicle. The *Melanerpeton* type, in fact, appears to have been a larval rhachitome, probably the young of *Chelydosaurus* found at the type locality, and our material requires a new designation. We herewith apply to it *Phaiherpeton*, gen. nov., genotype *"Melanerpeton" pulcherrimum* Fritsch. The widely open otic notch and the characteristic proximal enlargement of the stem of the interclavicle may be given as diagnostic characters of this genus of the Seymouriamorpha.

It seems certain that we are, in this *Phaiherpeton* material, dealing with a member of the Seymouriamorpha. The basic pattern of the skull table is that of the anthracosaurs; the neural arch structure, the interclavicle, etc. are diagnostic of the seymouriamorphs rather than the embolomeres, even in default of evidence of vertebral build.

The small size, feeble ossification, the skull proportions, and the possible presence of gill remnants in a few specimens indicate that we are dealing with aquatic animals, presumably larval forms. The absence in these deposits of larger tetrapods of similar build which might be identified as the adult *Phaiherpeton* suggests that this genus may have been paedogenetic. However it may simply be that the type of deposition was such that it was unsuitable for the entombment of adults — which may have been more terrestrial in habits. We may note, for example, the presence in the Bohemian Permian of a primitive tetrapod, *Sphenosaurus sternbergii* (Fritsch 1901, vol. 2, p. 28, pl. 59, etc.), with a similar type of vertebrae — although *Sphenosaurus* (of which the skull is unknown) is very probably a true reptile. No other amphibia of any sort are known from the Boskovice furrow; from the Broumov region, the only large forms are *Chelydosaurus* and *Lusor*. The former, however, is clearly a rhachitome. The latter is here tentatively assigned to the same group. But it will be noted that diagnostic features are not clear; it is not altogether impossible that *Lusor*, despite the great differences from *Phaiherpeton* in skull proportions, might prove to be a related or identical seymouriamorphan if better known.

The widely open otic notch and the seemingly comparable vertebral structure bring to mind the *Diadectes* group of cotylosaurs. These forms are, however, universally regarded as true reptiles, and there is at present little reason to associate them with the small amphibians here discussed.

Discosauriscus

(Figs. 12, 14, 47)

Discosaurus permianus was described by Credner (1883, p. 294–300, pl. 12, figs. 6–11; 1890, pp. 258–77, pl. 10, figs. 8–10, pl. 11; 1891, figs. 10, 27, 39, 44) on the basis of several incomplete individuals from the lower Permian Niederhässlich locality near Dresden. *"Sparagmites" areiger* (Credner 1885, pp. 723–724, pl. 29, figs. 1, 2) is, as Watson notes (1942, p. 82), founded on a specimen from the same place with poorly preserved vertebrae of the same type. A further Niederhässlich specimen is the type of *"Melanerpeton" spiniceps* of Credner (1883, 289–293, pl. 12, figs. 3–5); material assigned to this species by Geinitz and Deichmüller (1882, pl. 7) pertains to *Acanthostoma*. Again, specimens figured by Credner in 1885 (pl. 27, figs. 2–4) as belonging to *Melanerpeton* appear to belong to the

present genus. Riabinin (1911) described, as *Discosaurus uetschajevi*, two small skeletons from Kargala, in the Orenburg region of eastern Russia, from beds in the lowest zone (Zone I) of the continental Russian Permian. The description is brief; but the scales are of the same type as that of the German material, and the other features known are comparable. Kuhn (1933, p. 52), noting that *Discosaurus* is preoccupied, has substituted *Discosauriscus* as a generic designation.

The *Discosauriscus* specimens are all those of small animals; skull lengths appear to have been on the order of 3 to 4 cm., the length to the sacrum probably 10 to 11 cm. The skull was short and broad; although the specimens are imperfect anteriorly and posteriorly, the roof pattern can be readily made out. It is of anthracosaurian and seymouriamorphan type, with an intertemporal, absence of supratemporal-postparietal contact, and a deep otic notch. The palate is poorly preserved. The *"Melanerpeton" spiniceps* type has a palate bearing pointed teeth of relatively large size.

The number of presacral vertebrae cannot be positively determined, but German and Russian specimens indicate a minimum count of 20 to 22. There was a single sacral. The neural arches are, as far as can be discerned, quite similar to those of *Seymouria*, with low rounded contours. The central structures are of interest. The "pleurocentra" are directly beneath the neural arches, in a fashion comparable to that of *Seymouria* and reptiles and appear to reach the ventral margin of the column; their structure thus approaches that of the typical seymouriamorphs and reptiles. Credner notes, however, that they are distinctly paired — a primitive condition, the retention of which in this case may, however, be due to immaturity or paedogenesis. The intercentra are much larger in area than those of *Seymouria* or *Kotlassia*, and form large crescents, or rather incomplete rings, reaching nearly to the top of the central area. The caudals appear to have retained a somewhat rhachitomous type of structure, comparable to that of *Pholidogaster*. The posterior ribs are distinctly double-headed; anteriorly the ribs are expanded proximally, but without indication of division of heads.

The interclavicle is of the stemmed type common to this group; the stem lacks the characteristic *Phaiherpeton-Kotlassia* expansion anteriorly. The ilium (Credner 1890, pl. 10, fig. 8) is low and expanded antero-posteriorly in the fashion of seymouriamorphs and primitive reptiles. Pubis and ischium were both ossified. The limbs, though short, were very stout. The digital formula cannot be determined. The Russian material indicates a higher phalangeal formula

than that of temnospondyls, for in the pes four successive phalanges give a count of 2.3.4.4, i.e., just short of the formula of *Seymouria* and reptiles for the first four toes.

A most characteristic feature of the genus, and the one from which the name stems, is the nature of the preserved squamation. The scales are circular and show a series of concentric lines of ossification rather similar to those of the flanks of *Eryops*, etc., and the modern Apoda. There are no described remains of normal ventral scales, and it is possible that this type of circular scale was the only sort retained by *Discosauriscus*.

It seems certain that, as Watson (1942, p. 82) has pointed out, *Discosauriscus* is a seymouriamorph, a European contemporary of *Seymouria*. The short head and feeble ossification of the skeleton may indicate that the known specimens are the young of a form which reached a larger size as an adult, but may also be indicative of a degenerative process leading to the conditions seen in *Kotlassia* of the later Permian of the same continent and in the contemporary *Phaiherpeton*. The vertebral structure is of importance as showing the manner in which the seymouriamorph and reptilian vertebral type have evolved from a rhachitomous structure. The large intercentra, and pleurocentra which, despite their size, are unfused at the ventral margin, show an ideal intermediate condition. But while these specimens show an intermediate morphological stage, *Discosauriscus* may be paedogenetic rather than truly primitive in this regard.

Diplovertebron

(Figs. 12, 14, 46)

It is with hesitation that we place here a genus which shows features of both embolomeres and seymouriamorphs. *Diplovertebron punctatum* is a small tetrapod not uncommon in the Pennsylvanian Gaskohle of Nýřany, Bohemia. Fritsch (1901, vol. 2, pp. 11–13, pls. 50, 52, 53; cf. Steen 1938, p. 239) figures various specimens showing a large array of disarticulated elements. Watson (1926, pp. 238–241, figs. 29–31) figures and describes a small, nearly complete skeleton, and points out that the skull and partial skeleton described by Jaekel (1902; 1911, fig. 150, etc.) as *Gephyrostegus bohemicus* is apparently the same.

The skull roof pattern is that of a typical anthracosaurian in all respects, including the typical tabular, presence of an intertemporal,

well developed otic notch and, apparently, a rather loose attachment of the cheek in primitive embolomere fashion. The face is much shorter, relatively, than in the characteristic late Carboniferous embolomeres, and in this regard is closer to the seymouriamorphs. The tabulars lack the characteristic embolomere "horns." There is a well developed ring of some 33 sclerotic plates.

Little is known of the palate except that there were large pterygoids covered with denticles. Watson states that in the lower jaw there is a long prearticular extending nearly to the symphysis, and that all three coronoids were tooth-bearing. There is no mention of the large vacuities present on the inner surface of the jaw in typical embolomeres; one may assume that they were absent.

The postcranial material is rather poorly ossified and few details can be made out. There appear to have been about 25 presacral vertebrae; Watson was unable to distinguish a specific sacral vertebra and suggests that a primitive unspecialized condition was present. The vertebral structure is of interest. As seen in lateral view (Fig. 12), the caudals — the only vertebrae well preserved — appear to show, as the name of the genus indicates, a typical embolomerous condition. However, as Steen notes, the intercentra, despite their height and dorsal breadth, as seen in side view, are not complete rings, but are incomplete dorsally. This condition is technically that of the Seymouriamorpha. It may, however, be possible that this appearance (cf. *Calligenethlon*) is due to immaturity, and that a complete ring was formed by a cartilaginous dorsal connection between the two sides.

Unfortunately the dorsal vertebrae are not well known, and hence there is no proof as to whether the neural arches were of the more normal type seen in typical embolomeres or of the swollen character of the seymouriamorphs.

The interclavicle is definitively of the type seen in seymouriamorphs and primitive reptiles, and it is identical with that of *Phaiherpeton* (*"Melanerpeton"*) and *Kotlassia*. As figured by Fritsch, there is a broad rounded head with a serrate anterior border and little sculpture, and a long stem, the anterior portion of which is distinctly swollen. The clavicle, Jaekel notes, is little expanded; a typical cleithrum is present. In the endochondral girdle, only a scapula is reported. In the pelvis the pubis is unossified in known material. The ilium is of the primitive type seen in the embolomeres with (as preserved) a small dorsal expansion and a well-developed rod-like posterior extension. The limbs, as in typical seymouriamorphs, are short but

stout. Little detail is seen in the limb bones; there appears to be no entepicondylar foramen in the humerus. Carpus and tarsus are unknown. A perfectly preserved manus shows five digits with a formula of 2.3.3.3.4; the hind foot is incomplete but possessed five digits. A typical labyrinthodont ventral scale-system was present.

Diplovertebron is an animal of great interest, definitely an anthracosauroid type but hard to place as regards assignment to the embolomeres, where Watson would locate the genus, or to the seymouriamorphans, with which there are points of resemblance. A reasonable interpretation is one which considers *Diplovertebron* as a primitive seymouriamorphan, in process of evolution from the common ancestors of that group and the typical later embolomeres. Under this interpretation such features as the large but incomplete intercentra, the possible lack of a coracoid, the shape of the ilium, the lack of a specialized sacral rib (if confirmed) and the loose attachment of skull table and cheek are all primitive features inherited from primitive ancestors. The five-toed manus and the phalangeal formula may well be primitive, but evidence is lacking; the relatively short face is presumably a primitive feature retained in seymouriamorphs; the long-stemmed interclavicle is a definite mark of the seymouriamorphan. We may note in passing that despite the seemingly generalized nature of this genus, there is no indication in the skull table of any tendency toward the true reptilian pattern.

The position of this genus must remain doubtful until a well-preserved vertebral column, exhibiting diagnostic features, is discovered.

Solenodonsaurus

We shall conclude this section by a discussion of a few forms which appear to lie close to the boundary between seymouriamorphans and reptiles, but which on the whole appear to be more appropriately placed, until better known, in a reptilian (cotylosaurian) category.

Solenodonsaurus janenschi has as a type a skeleton from the gas coal of Nýřany, Bohemia; its occurrence at this horizon is of interest, for if the genus is reptilian, it is among the oldest known members of that class. The type slab was mistakenly ascribed by Broili (1905, pl. 1) to the rhachitome *Cochleosaurus*; the fortunate discovery of the reverse slab (Broili 1924) proved the animal was generically distinct. A second specimen consists of fragmentary remains of an individual described by Pearson (1924). Broili designated *Solenodonsaurus* as

a cotylosaur; Pearson pointed out features which suggested inclusion in the Seymouriamorpha.

The anterior part of the column shows vertebrae which, with stout centra and reduced and feebly ossified intercentra, indicate that *Solenodonsaurus* is either a true reptile or a seymouriamorphan, and the stage of reduction of the intercentra is suggestive of the reptilian alternative. It is stated by Pearson that the neural arches are of the swollen type seen in both groups concerned, but there appears to be some doubt of this (cf. Romer 1925, p. 462; White 1939, p. 399). The humerus and much of the shoulder girdle are known, but do not give a basis for decision.

In Broili's specimen the skull is complete but little known as to detail. The general contours, the rather long and slender face and — particularly — the grooved but nonlabyrinthine dentition suggest reference to the reptiles. Pearson's specimen shows various individual elements of the facial region, but the morphology here is not decisive. The diagnostic differences between true cotylosaurian and seymouriamorphan skulls are to be sought in the temporal-otic notch region. Here the material is, unfortunately, none too good and capable of varied interpretations. In the type no sutures are visible in the temporal region or table. The specimen shows, as figured, a general concavity at the posterior end of the cheek region which might be considered as an otic notch. But this does not have the form, apparently, of a seymourian notch, but rather suggests the beginning of a diadectid type of notch, which, as I have suggested elsewhere, may be a secondary, reptilian formation. The Pearson specimen includes a disconnected cheek and temporal region which, as figured, shows a different situation, with a small but deeply cleft notch. The sutures, as interpreted by Pearson, do not agree well with either seymouriamorphans or primitive cotylosaurs, although the absence of an intertemporal, if confirmed, is a distinctive reptilian feature.

Until better material is obtained, it is impossible to correctly assign *Solenodonsaurus*, but at the moment the weight of evidence suggests that the genus is truly reptilian and perhaps not distantly related to *Limnoscelis*.

Eusauropleura

This is known only from a single specimen of *E. digitata* from the Pennsylvanian of Linton, Ohio (Cope 1875, p. 403, pl. 37, fig. 1; Moodie 1916, pp. 157–158, pl. 20, fig. 4; Romer 1930, pp. 135–137, fig. 26). This shows the ventral armor and limbs of a tetrapod of

some sort; unfortunately no trace of head or of girdles is visible. The manus, with quite elongate phalanges, has a formula of 2.3.4.5.3. This high count (although equalled in *Seymouria*) and the long joints suggest a reptile rather than a seymouriamorphan.

Tuditanus

Tuditanus punctulatus or *"Eosauravus copei,"* from the Pennsylvanian of Linton, Ohio, has been discussed by various writers since the days of Cope, including Williston (1908), Moodie (1909, pp. 11–16, pls. 4, 5; 1916, pp. 85–86, fig. 19) and the writer (1930, pp. 134–135). There are two specimens, which Cope believed specifically identical; Williston, however, believed them unrelated and considered the second to belong to a primitive reptile, *Eosauravus*. The stemmed interclavicle, the seemingly broad-arched vertebrae and the pes with rather elongate phalanges and a formula of 2.3.4.5.4 indicate either a seymouriamorph or cotylosaur, but which of the two cannot be determined.

Adenoderma

This genus is really quite indeterminable; the only specimen is the holotype of *A. gracile* (Fritsch 1901, p. 126, pl. 19, fig. 1) from the Gaskohle of Třemošná near Pilsen. This is a very poorly preserved skeleton, about which is seemingly a skin impression. About 22 vertebrae are indicated and some remains of short but stout limbs. The vertebral impressions appear to show broad neural arches; this fact gives some slight reason for assignment to the Seymouriamorpha.

DISCUSSION

Seymouria and *Kotlassia* are, as has been long recognized, closely related genera and form the basis for Watson's establishment of the group Seymouriamorpha (Watson 1917, p. 171), originally considered a subdivision of the Cotylosauria. The group, however, appears to have included still other forms. Watson recently (1942) noted that *Discosauriscus* was seymouriamorphan in nature, a conclusion which the writer had also reached. *Phaiherpeton*, as we have seen, appears to consist of larval or paedogenetic forms of the same sort; and, as discussed above, *Diplovertebron*, usually considered an embolomere, may be an older and more primitive member of the same group. The known life span of the Seymouriamorpha is thus from

the latter part of the Pennsylvanian (*Diplovertebron*) to the late Permian (*Kotlassia*). The group is, therefore, as far as known, a relatively late one.

That the Seymouriamorpha are closely related to the embolomeres seems clear. They agree with that group in a number of features in which there is marked contrast with typical temnospondyls. These features include: large tabular articulating with parietal; both internal and external nares relatively close to one another; vomers narrow; lateral walls of braincase with marked gap between sphenethmoid and otic capsule; carotid passing medial to basipterygoid processes; complete ring-shaped true vertebral centrum. There are a considerable number of other features in skull and limb construction in which it is probable that embolomeres and seymouriamorphs agree, but for which proof is impossible until the embolomeres are better known.

A further suggestion of relationship is afforded by the structural conservatism exhibited by both embolomeres and seymouriamorphs. Permian members of both groups show a number of primitive features lost by most or all of their temnospondyl contemporaries. These features include: the retention of the intertemporal bone; small interpterygoid vacuities; movable basal articulation of braincase and palate; single occipital condyle; entepicondylar foramen in humerus; posterior elongation of ilium.

Diagnostic differences between embolomeres and seymouriamorphs are few in number, as far as we can determine at the present time; they may, however, be increased when embolomere structure is better known. Apart from *Diplovertebron*, the seymouriamorphs show a rounded otic notch and a cheek region solidly united to the skull roof, in contrast to the slit notch, presumably more primitive, and loose attachment of cheek and skull seen in embolomeres. The tabular horn of embolomeres is absent in the seymouriamorphs. The lateral vacuity in the braincase between otic capsule and sphenethmoid is much more highly developed than in embolomeres. The better-known seymouriamorphs have a peculiar lateral expansion of the braincase surrounding the fenestra ovalis; this appears to be lacking in the embolomeres. The highly developed jaw fenestrae of typical embolomeres are absent in seymouriamorphs.

The limbs are much stouter in seymouriamorphs than in known embolomeres. The stemmed interclavicle of seymouriamorphs may be a useful key character, but we have as yet little proof of its general absence in embolomeres. Iliac expansion in embolomeres is confined to the anterior end of the potential blade.

Vertebral construction is a major and significant feature by which the two groups are sharply differentiated. The swollen arches of seymouriamorphs, very similar to those of early reptiles, are unknown in embolomeres. Both groups have a complete true centrum, but the intercentum of seymouriamorphs is a persistently primitive ventral crescent. In this last feature, we have noted, the Seymouriamorpha are apparently the more primitive group of the two.

That the two anthracosaurian groups are descended from common ancestors is clear, and such ancestors were presumably among the earlier Carboniferous types which we have above included for the time being among the Embolomeri despite the probability that the construction of their vertebral centra was by definition seymouriamorphan rather than truly embolomerous.

It is generally agreed that the Seymouriamorpha, particularly as represented by the typical genus *Seymouria*, are morphologically close to the dividing line between amphibian and reptilian structural stages, and the systematic position of the group has been a matter of debate. Broom has consistently maintained that *Seymouria* should be assigned to the amphibians, and Sushkin took the same position; Broili, Williston, Watson and the writer, among others, argued for its inclusion among the reptiles. Recently White (1939), although admitting the lack of clear-cut evidence, decided in favor of the reptiles for *Seymouria*; but on the other hand Bystrow (1944), on the basis of his study of *Kotlassia*, believes the group to be amphibian; Watson (1942, p. 83) has reversed his former decision, and the writer (Romer 1946) has also come to believe in the amphibian nature of the seymouriamorphs.

The Seymouriamorpha, particularly *Seymouria*, show many features which we customarily regard as reptilian rather than amphibian in nature. One feature of this sort which is definitely diagnostic is the nature of the swollen neural arches, in which *Seymouria* shows almost absolute identity with the cotylosaurs. In addition to this, there are nearly a score of other reptilian features not commonly found in fossil amphibians. Such are: (1) presence of a lacrimal duct; (2) possession of five digits in the manus; (3) phalangeal formula (in *Seymouria*) of 2.3.4.5.3 or 4; (4) wide gap in the lateral wall of the braincase; (5) a supraoccipital bone ("*Conodectes*"); (6) a stemmed interclavicle; (7) a separate coracoid ossification; (8) expanded iliac blade; (9) combination of crescentic intercentra with "complete" true centra beneath neural arch.

There are, however, numerous features in seymouriamorphans which are definitely below the level of any typical reptile, and seem essentially amphibian. These include: (1) prominently sculptured skull; (2) paired postparietals; (3) tabulars and postparietals broadly exposed on flat skull table; (4) intertemporal present; (5) three coronoids and two splenials in lower jaw; (6) labyrinthine teeth; (7) large number of sclerotic plates. It might be argued, however, that since these are primitive features which would be expected in a reptilian ancestor at some stage or other, they merely show that the seymouriamorphs are more primitive than other reptiles, and do not necessarily prove that they were still amphibians.

Two further lines of evidence are available. One has to do with the hearing apparatus. I have pointed out (Romer 1946) that the elimination of the otic notch appears to have taken place in reptiles by the folding together of the sides of a slit-like notch of embolomere type; the exaggerated but rounded notch of seymouriamorphans does not fit this picture. The primitive reptilian stapes is an elongate structure with a markedly forked dorsal process; that of seymouriamorphans is of the very different normal amphibian type. The fenestra ovalis of seymouriamorphs is situated on a pronounced lateral extension of the otic capsule; no such structure is present in primitive reptiles.

The crucial point is, of course, the mode of development, where it can be ascertained. By definition a reptile is a form which lays an amniote type of egg and has thereby eliminated the aquatic larval stage from its life history. *Seymouria* and *Kotlassia*, as their most recent describers believe, appear to be terrestrial types as adults; but even in these genera there are suggestions that an aquatic larval stage was present. The traces of lateral line grooves reported by White in *Seymouria* are difficult to interpret unless the animal had an aquatic larval stage in which lateral line organs functioned. The general build of *Kotlassia* shows parallelism to later temnospondyls in a degree of skeletal degeneracy which in the latter is definitely associated with paedogenetic retention of features found in an aquatic larva. In *Phaiherpeton* there are reports of traces of gill structures. These, however, are not beyond doubt. Nevertheless the whole assemblage of material of this genus strongly suggests that we are dealing with water-dwelling animals, either larval or paedogenetic.

The evidence thus strongly indicates, although it does not prove, that the seymouriamorphs were non-amniotes. On the other hand we have noted features indicating that they are closely related to the

reptiles. Can they be considered as direct ancestors? Not, certainly, the known and characteristic genera of the group. We have noted peculiarities of the otic region which seem to debar them from such a position. I have recently (Romer 1946) discussed the structure of *Limnoscelis*, an archaic reptile which I believe to lie close to the base of that class. This form exhibits a pattern of the skull table which seems diagnostically reptilian, and is not found in known seymouriamorphans. In this pattern the intertemporal has been lost, and parietal and postorbital (much as in ichthyostegids) meet anterior to the supratemporal; the latter element remains wedged anteriorly into the lateral expansion of the parietal and runs back along the erstwhile margin of the vanished otic notch between tabular and squamosal to the posterior margin of the skull. An anthracosaur with this arrangement of skull elements developed, or in process of development, would be a proper reptilian ancestor. None such is known. When or if such a form is identified, it will presumably be found to be very similar to the Seymouriamorpha in most other features, and it might well prove possible to so define that group as to include such a reptilian ancestor.

CLASSIFICATION

In previous sections we have presented data and conclusions bearing on the relationships and phylogeny of the various groups here assembled in the Labyrinthodontia. This material may be summarized here in the attempt to formulate a provisional classification and scheme of phylogeny of the Labyrinthodontia.

That the labyrinthodonts early separated into two major groups, of which embolomeres and rhachitomes are typical representatives, seems clear. Their distinctive features are readily seen, not merely in such superficial characters as the contours of the tabular but in more basic features of braincase, palatal, and vertebral construction; it is probable that increasing knowledge of embolomere anatomy will emphasize rather than lessen the marked contrasts between the two groups.

Names definitely attached to these two units in unambiguous fashion are unfortunately not available. For the embolomeres and their reptile-like kin, Watson's term Anthracosauria (used by him for the embolomeres as here constituted) may be broadened to include the related seymouriamorphs. For the rhachitomes and related and

derived types, including the stereospondyls, no current term can be used without some danger of ambiguity. Although most of the included groups are (or may be assumed to be) rhachitomous in vertebral structure, it would be too great a stretch of customary usage to apply the term Rhachitomi to this larger assemblage. Objections to this use of the old term Temnospondyli are less valid. Temnospondyli was at one time widely used in much the sense of the current Labyrinthodontia. But seymouriamorphs were not included; little was known of embolomeres; the conception of the temnospondyls then prevalent was essentially that of the group to which we propose to restrict its use.[1]

Since the term Labyrinthodontia cannot be raised to a grade higher than that of a superorder without doing violence to any reasonable scheme of amphibian classification, Anthracosauria and Temnospondyli cannot be raised above ordinal status.

Our knowledge of the Ichthyostegalia is at present extremely limited, but the evidence strongly suggests that they are more closely related to the temnospondyls than to the anthracosaurs and hence should be included, as a suborder, in the Temnospondyli. As discussed earlier, the ichthyostegals, despite their early appearance and the probability that they were a common labyrinthodont stock in the late Devonian and early Carboniferous, cannot be considered as in any way ancestral to later labyrinthodonts in general or to later temnospondyl types. Their possible relationship to the lepospondyls is worthy of consideration.

It seems certain that, if the ichthyostegals be so included, the remaining temnospondyls form a single phylogenetic unit balancing them in a dichotomy. One is tempted to give a subordinal title to the remaining temnospondyls. But while a procedure of this sort is in a sense logical, it often results in taxonomic absurdities, and this would seem to be the case here. The non-ichthyostegal temnospondyls, in the course of their history, evolved into a wide variety of structural types, from forms like *Loxomma* and *Edops* on the one hand, to diversified end forms such as *Trematosaurus*, *Plagiosaurus*, *Metoposaurus* and *Cyclotosaurus* on the other. As a practical matter we have here assembled this diversity of forms into three units. We have "salvaged" for use as suborders the old terms Rhachitomi and Stereospondyli, although with some change of content and definition, and have added a third subordinal term, Trematosauria, for the Triassic

[1]Abel (1919, p. 271), we note, did use it to the definite exclusion of the embolomeres.

trematosaurs which appear to have obtained an advanced structural condition independently of the other "stereospondylous" types.

In the Rhachitomi we have placed all the more primitive members of the group, including all forms from the Carboniferous and early Permian. As in the case of any group of this sort, including a basic

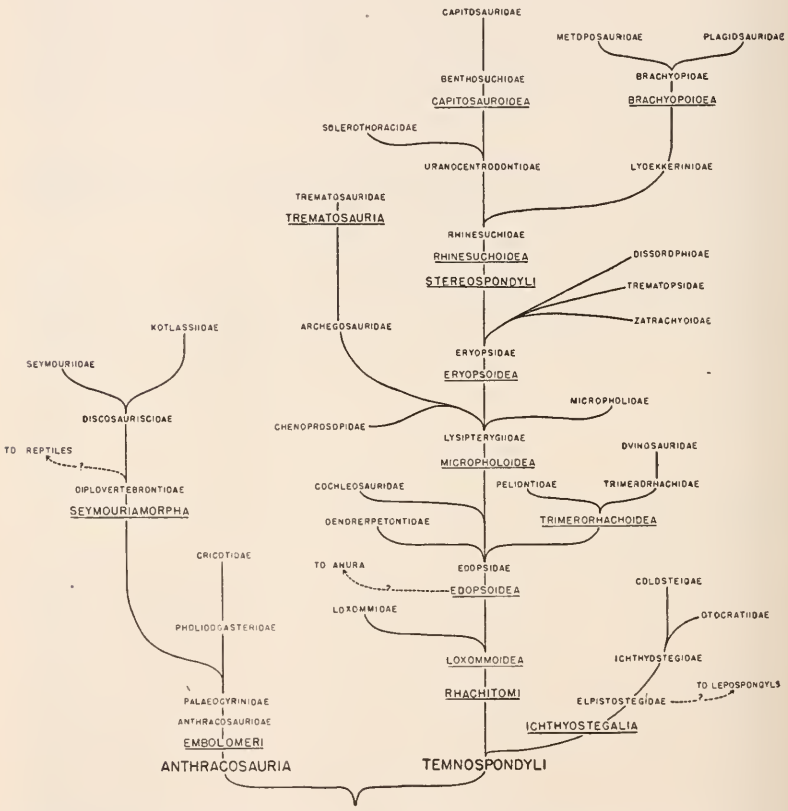

Fig. 48. Diagrammatic arrangement of the labyrinthodont families in the form of a provisional family tree.

stock and varied side branches not important enough to merit independent status, definition is difficult. Better definition is attained by the erection within the Suborder Rhachitomi of a series of superfamilies which are here regarded as representing successive evolu-

tionary grades: Loxommoidea, Edopsoidea, Micropholoidea, Eryopsoidea, with the Trimerorhachoidea as a side-branch of the second of these groups.

As noted by earlier writers, there is no proof that the loxommids of the Carboniferous are embolomerous; their organization, as far as known, agrees well with that of other temnospondyls. Their palatal and occipital structure is extremely primitive, and the Superfamily Loxommoidea may be regarded as a basal rhachitomous stage, through which (although not through the specialized Loxommidae) the ancestral rhachitomes may have passed in late Devonian and early Carboniferous times.

Edops of the earliest Permian appears to be a late survivor of a group of primitive rhachitomes a bit more advanced than the loxommids in palatal construction but still very primitive in such features as the single occipital condyle, movable basal articulation, retention of intertemporal, etc. Similar types occur in the Pennsylvanian, and may be grouped with *Edops* to form a Superfamily Edopsoidea. In both Pennsylvanian and Permian there are a number of genera which are obviously non-primitive in their short faces, depressed skulls and other features suggestive of the Triassic brachyopoids. They nevertheless retain many of the primitive features of the edopsoids and may, as the Trimerorhachoidea, be considered as an offshoot of that group.

A major step upward from the edopsoids would take us to *Eryops* and its kin, the characteristic rhachitomes of the early Permian. There are, however, certain genera of the late Pennsylvanian and Permian which appear to represent a half-way stage between these major "grades" of temnospondyl development. These we shall term the Superfamily Micropholoidea, taking the name from a late-surviving member of the group. In these forms the intertemporal bone has been lost, as in all more advanced temnospondyls; but the basal articulation is still movable and the occipital condyle tends to retain its primitive structure. Apart from specialized, long-snouted genera of the early Permian, such as *Archegosaurus* and *Chenoprosopus*, we can at present include here only a single genus each from the late Pennsylvanian, early Permian and basal Triassic. Possibly the micropholoids may prove to be common and characteristic of some Pennsylvanian stage in temnospondyl development; equally possible, it may prove that the micropholoid group had little real existence, and that various edopsoid descendants passed independently through this morphological condition on their way to or toward the eryopsoid level.

Eryops is *par excellence* the typical rhachitome, and with numerous types exhibiting similar characters may form the Superfamily Eryopsoidea. There are a number of distinctly advanced features. Not only has the intertemporal disappeared, but the condyle has developed to, or far towards, a double condition; the interpterygoid vacuities are moderately large, the basal articulation has lost its motility although the connection between palate and braincase is a slender one. Forms of this sort are the characteristic amphibians of the early Permian, including, besides the eryopsids as a seemingly central stock, such common types as the dissorophids, zatrachyids and trematopsids; there are, however, apparent fore-runners in the late Pennsylvanian.

It is among the eryopsoids that we find the temnospondyls most highly adapted to a terrestrial existence. Some of the more primitive members of the group were in great measure if not entirely aquatic, and presumably primitively so. But *Eryops*, with stout if short limbs, was readily able to be semi-terrestrial in habit, the trematopsids likewise; and the dissorophids, one may believe, may have been primarily land dwellers. From this point on, however, the history of the temnospondyls is one of a regression toward a purely aquatic benthonic existence.

The trematosaurs, long-snouted fish eaters, perhaps marine, of the early Triassic are usually considered as stereospondyls or at least brigaded with components of that group. They are, however, persistently rhachitomous in vertebral structure (the pleurocentra may remain cartilaginous but were obviously large, even so). On the other hand, they have, like the other Triassic groups, "progressed" (in a degenerative fashion) far beyond the level of the rhachitomes in numerous features of the braincase, basicranial region, etc. It seems certain, however, that these progressive features were acquired in a parallel development to other Triassic families, and that they have arisen independently from Permian rhachitome ancestors (presumably the *Archegosaurus* group). It therefore seems reasonable to erect for them a separate suborder, the Trematosauria.

In such an ascending series as that leading from primitive rhachitomes to advanced Triassic temnospondyls, any point at which a major cleavage is made is necessarily somewhat arbitrary. The Permian neorhachitomes such as *Rhinesuchus* are not far beyond the eryopsoids; we will, however begin the Stereospondyli with the early neorhachitomes since the diverse groups forming the Triassic components of the suborder cannot have had a common ancestor at any

more advanced stage. It may be argued that it is improper to include such neorhachitomous forms in a group of which the name implies the possession of stereospondylous vertebrae; but it may be pointed out that most of the capitosaurs, always considered a major element of the stereospondyls, did not possess a truly stereospondylous vertebral structure.

The term "neorhachitome" has been usefully applied to a series of late Permian and basal Triassic genera structurally transitional between the eryopsoids, on the one hand, and the Triassic capitosaurs etc. on the other. The more primitive neorhachitomes, mainly from South Africa, with a more generalized skull shape and rather primitive characters, are here grouped as the Superfamily Rhinesuchoidea, and perhaps include the common ancestors of the later stereospondyls.

The capitosaurs of the Triassic appear to form the termination of the "main line" of temnospondyl evolution, from edopsoids and eryopsoids up through the rhinesuchoid group. If the Superfamily Capitosauroidea be erected for their reception, it is seen that *Benthosuchus* and allied advanced neorhachitomes (mainly from the Russian basal Triassic) must be included in the same group, as closely allied with, ancestral to, and hardly separable from the capitosaurs.

Very different in nature from the capitosaurs are the short-faced brachyopids of the early Triassic and their presumed descendants, the very short- and broad-skulled plagiosaurs, with true stereospondylous vertebrae. These two families are conveniently united in a Superfamily Brachyopoidea. Study indicates that the metoposaurs of the late Triassic, despite the elongate post-orbital segments of their skulls, are similar in many features to these forms and may well be included in the same group. The descent of brachyopoids from Permian trimerorhachoids (*Trimerorhachis, Dvinosaurus*) has been advocated, and this theory still merits consideration. We have noted, however, factors which suggest that the resemblances are due to parallelism, and here adopt provisionally the view that the brachyopoids have sprung from primitive neorhachitomes of the rhinesuchoid group.

Less rich in numbers than the temnospondyls but more imporant in phylogenetic potentialities are the forms here included in a second major group of labyrinthodonts, here termed the Anthracosauria. These include very primitive amphibian types and, it is generally agreed, are related to the ancestry of reptiles. There are numerous points of difference between anthracosaurs and temnospondyls, and we have noted that many of the diagnostic characters of the Anthracosauria are reptilian in nature.

The basal stock of the anthracosaurs are the Embolomeri, here treated as a suborder. Watson has rightly emphasized the many primitive features of the group, and they are certainly very primitive amphibians, even though the position given them here is not as basal as that to which that writer would assign them. Some of the more primitive forms — unfortunately poorly known — may be close to the ancestry of seymouriamorphs and reptiles. However the later — and better known — genera, such as *Pteroplax* [*Eogyrinus*] and *Archeria* ("*Cricotus*"), are members of a group of persistently aquatic fish-eaters.

Seymouria and its relatives, long in debate as regards their phylogenetic position, are here considered as on the amphibian side of the dividing line, and to constitute the Suborder Seymouriamorpha of the Anthracosauria. They are clearly allied to the embolomeres and may have sprung from primitive members of that group. They are, on the other hand, clearly allied to the reptiles, but the typical seymouriamorphs are too specialized to be actual ancestors of the primitive cotylosaurian reptiles.

Below, the data of the preceding systematic sections are summarized in a formal classification and an accompanying phylogenetic chart (Fig. 48). It cannot be too strongly emphasized that both classification and phylogeny are purely provisional in nature, and not to be considered as in any way definitive, in general or in detail. I have merely attempted to present the most reasonable conclusions to which a consideration of the evidence currently available leads us. In the past, however, new material has more than once upset reasonable conclusions based upon seemingly satisfactory evidence; and there is no warrant that similar reversals will not occur in the future.

CLASS AMPHIBIA

SUBCLASS APSIDOSPONDYLI

Vertebral centra primitively formed by cartilaginous arcualia or ossifications formed about them, rather than by perichordal ossification.

Superorder Labyrinthodontia

Primitive apsidospondyls in which centra are formed by arch elements (pleurocentra or intercentra or both) and anuran specializations are lacking.

ORDER TEMNOSPONDYLI

Vertebrae generally rhachitomous; pleurocentra typically paired latero-dorsal structures, never forming complete discs and sometimes lost. Tabular not in contact with parietal. Vomers broad, widely separating internal nares. Laterosphenoid region of braincase completely walled by bone or cartilage. ?No supraoccipital bone. Manus with four digits.

Suborder Ichthyostegalia. Intertemporal absent; postfrontal widely separated from supratemporal. Post-orbital region (including tabulars) elongate, face relatively short. Nares close to margin of skull. Quadrate not markedly behind level of occiput. Palatal teeth in pairs. Basal articulation movable.

Elpistostegidae. Postparietals paired, greatly elongate. Palate unknown, presumably closed. *Elpistostege*, early U. Dev., N. A.

Ichthyostegidae. Postparietal unpaired, moderately elongate. Palate closed. *Ichthyostega*, *Ichthyostegopsis*, uppermost Dev. or lowest Miss., Greenland.

Otocratiidae. Postparietals paired, moderately elongate; otic notch closed. Palate unknown. *Otocratia*, Miss., Scotland.

Colosteidae. Postparietals paired, moderately elongate; otic notch open. Palatal vacuities large. *Colosteus*, *Erpetosaurus*, U. Penn., N. A.

Suborder Rhachitomi. Vertebrae typically rhachitomous, with pleurocentra moderately developed, intercentra usually crescentic and not surrounding notochord. Intertemporal present or absent; parietal not in contact with postorbital. Posterior elements of skull in general not elongate. Skull usually not greatly flattened. Parasphenoid usually not flattened in cultriform process nor expanded or flattened posteriorly. Basal articulation movable or fused; if fused, the area of union not expanded, and exoccipital plays no part in articulation. Palatal fangs usually confined to three typical pairs, without development of connecting rows. Braincase usually well ossified except in small or immature animals. Condyle single, triple or double, but if double, the members of the pair not widely separated. Opisthotic forms most of paroccipital bar. Descending flanges of postparietals and tabulars not greatly developed. Jaw articulation usually well back of level of occiput. Occipital plate essentially vertical.

Superfamily Loxommoidea. Intertemporal primitively present. Palate closed. Movable basal articulation. Occipital condyle single. Quadrate markedly posterior to level of skull condyle.

Loxommidae. Orbital opening expanded anteriorly as keyhole-shaped structure. *Loxomma,* U. Miss. — U. Penn. Eu.; *Baphetes,* L. Penn. Eu., M. Penn. N. A.; *Macrerpeton,* Penn. N. A.; *Megalocephalus* [*Orthosaurus, Orthosauriscus*], L.-M. Penn. Eu.; *Spathiocephalus,* U. Miss. Eu.

Superfamily Edopsoidea. Intertemporal present. Interpterygoid vacuities present but relatively small; pterygoid reaches forward to vomer. Movable basal articulation. Occipital condyle single. Quadrate well behind level of occipital condyle. Face moderately long.

Edopsidae. Interpterygoid vacuities very small; pterygoids meet anteriorly. Otic notch not prominently developed. *Gaudrya,* U. Penn. Eu.; *Leptophractus,* U. Penn. N. A.; *Edops,* L. Perm. N. A.; *?Lusor,* L. Perm. Eu.

Dendrerpetontidae. Interpterygoid vacuities of moderate size, pterygoids here (and in all later families of temnospondyls) fail to meet anteriorly. Otic notch prominently developed. *Dendrerpeton* [?incl. *Dendryazousa, Dendrysekos, Platystegos,* M. Penn. N. A.

Cochleosauridae. Palatal vacuities larger. Occipital condyle tending toward paired condition. *Cochleosaurus,* U. Penn. Eu.

Superfamily Trimerorhachoidea. Interpterygoid vacuities enlarged. Quadrate close to level of occipital condyle. Face short. Palatal teeth may be arranged in rows connecting primitive tusk pairs. Other features as in edopsoids.

Peliontidae. Skull short. Tabulars much reduced. ?Larval or paedogenetic forms. *Eugyrinus, ?Erpetocephalus,* M. Penn. Eu.; *Pelion,* U. Penn. N. A.; *?Cephalerpeton, Mazonerpeton, Micrerpeton, Ericrpeton,* U. Penn. N. A.

Trimerorhachidae. Very long skull table; skull much flattened. Otic notch not prominent. Large interpterygoid vacuities. Broad cultriform process of parasphenoid. Marginal teeth small but numerous. Dermal shoulder girdle greatly expanded ventrally. Body flattened. Limbs small. Neotenous. *Saurerpeton,* U. Penn. N. A.; *?Dawsonia,* U. Penn. Eu.; *Trimerorhachis,* L. Perm. N. A.; *Chalcosaurus,* L. Perm. Russia.

Dvinosauridae. Post-orbital part of skull not as elongate as in last family. Intertemporal fused with postorbital. Condyle tending to double condition. Dermal girdle less expanded. *Dvinosaurus,* U. Perm. Russia.

Superfamily Micropholoidea. Rhachitomes advanced over the edopsoid condition in loss of intertemporal element, but basal articulation movable and occipital condyle typically single. Interpterygoid vacuities moderately large. Jaw length variable.

Lysipterygiidae. Skull shape normal. Lacrimal in contact with frontal. Pterygoid reaches vomer. Quadrate about on level with occipital condyle. *Potamochoston,* U. Penn. Eu.; *Lysipterygium,* L. Perm. India.

Micropholidae. Skull shape normal except otic notch enlarged. Pterygoid does not reach vomer. Quadrate about on level with occipital condyle. Palatal teeth tending to develop in rows. Condyle more or less tripartite. *Micropholis,* L. Trias, S. Afr.

Chenoprosopidae. Antorbital region of skull much elongated, muzzle broad. Choanae elongate. ?*Mytaras,* U. Penn. N. A.; *Chenoprosopus,* L. Perm. N. A.

Archegosauridae. Skull more or less elongate, with slender snout. Lacrimal approaches contact with frontal. Pterygoid does not reach vomer. Palatal teeth developed in rows. *Archegosaurus,* L. Perm. Eu., ?India; *Melosaurus, Platyops,* L.-M. Perm. Russia.

Superfamily Eryopsoidea. Advanced over micropholids in loss of motility in basal articulation and subdivision of condyle to tripartite or double condition. Interpterygoid vacuities of moderate size; pterygoids usually reach vomers and have moderately developed lateral flanges. Palatal teeth usually develop in primitive pairs. Quadrate moderately behind or on level of condyles.

Eryopsidae. Semi-terrestrial forms with stout limbs, body relatively high and narrow, head large, broad and moderately flattened. Otic notch not greatly developed. *Eryops,* L. Perm. N. A.; *Actinodon, Chelydosaurus, Onchiodon, Osteophorus, Sclerocephalus,* various "branchiosaurs", L. Perm. Eu.

Trematopsidae. As last, but otic notch greatly developed. Intercentra may form complete discs. ?*Mordex,* U.

Penn. N. A.; *Trematops, Acheloma, Parioxys,* L. Perm. N. A.

Dissorophidae. Terrestrial forms with stout limbs, body relatively high and narrow, dorsal development of dermal armor. Skull high and narrow, face short. Otic notch greatly developed. Pterygoids do not reach vomers. Condyles paired. Quadrate about on level of condyles. *?Arkanserpeton, ?Platyrhinops,* U. Penn. N. A.; *Alegeinosaurus, Aspidosaurus, Broiliellus, Cacops, Dissorophus, Tersomius,* L. Perm. N. A.; *Zygosaurus,* L.-M. Perm. Russia.

Zatrachydidae. Aquatic or semi-aquatic forms. Skull depressed and broad. Muzzle greatly expanded and usually with fontanelle developed in dermal bones. Quadrate about on level of condyles. Limbs weak. *Stegops,* U. Penn. N. A.; *Zatrachys, Platyhystrix,* L. Perm. N. A.; *Acanthostoma, Dasyceps,* L. Perm. Eu.

Suborder Trematosauria. Aquatic (?marine) fish-eaters. Body poorly known but presumably long and slender, limbs reduced. Vertebrae rhachitomous, pleurocentra moderately large although sometimes persistently cartilaginous. Skull not depressed but relatively high and narrow; triangular in shape with pointed snout; frequently elongate both pre- and post-orbitally. Intertemporal absent, postfrontal and supratemporal in contact. Palatal vacuities large, pterygoid usually not reaching palatine; ectopterygoid as well as palatine elongate. Rows of palatal teeth developed, but large tusks on vomer and palatine. Body of parasphenoid developed as broad and elongate plate extending backward below occipital region; fused basal articulation exhibits long suture between parasphenoid and pterygoid. Exoccipital-pterygoid contact present but not visible ventrally. Paired occipital condyles, widely separated. Opisthotic does not take part in paroccipital bar. Otic and sphenoid regions of braincase feebly ossified. Exoccipital extends forward into otic region. Quadrate close to level of condyles.

Trematosauridae. Trematosaurus, L. Trias. Eu. (including Russia); *Tertrema, Aphaneramma, Platystega, Peltostega,* L. Trias. Spitzbergen; *Lyrocephalus,* L. Trias. Spitzbergen, ?Greenland; *Stoschiosaurus,* L. Trias. Greenland; *Trematosuchus, Rhytidosteus,* L. Trias. S. Afr.; *Gonioglyptus,* L. Trias. India.

Suborder Stereospondyli. Aquatic, mainly bottom dwellers. Pleurocentra reduced, seldom ossified and may be entirely absent; intercentra always highly developed and may form complete discs surrounding the notochord. Skull usually more depressed than in other suborders. Intertemporal absent; parietal not in contact with postorbital. Two distinct occipital condyles, widely separated, on exoccipitals. Large palatal vacuities; pterygoid does not reach vomer. Cultriform process of parasphenoid flattened; basicranial region flattened to a variable degree. Palatal teeth usually formed in rows. Braincase and pterygoid fused, the area of junction always more or less expanded anteroposteriorly and flattened ventrally. Braincase usually poorly ossified, even in large forms, and opisthotic almost always excluded from paroccipital bar. Exoccipital ossification extends forward into otic region. Quadrate typically about on the level of the occipital condyles or even in advance. Postcranial skeleton, where known, generally poorly ossified and limbs small.

Superfamily Rhinesuchoidea. Skull proportions of central temnospondyl type, without marked elongation of either preorbital or post-orbital regions; snout broadly rounded. External nares widely separated. Otic notch of normal type. Skull not greatly depressed. Interpterygoid vacuities moderately large; pterygoids reach forward to palatines, ectopterygoids short. Basicranial region and cultriform process relatively little flattened, the latter little expanded. Parasphenoid-pterygoid suture relatively short, exoccipital-pterygoid contact usually absent and not visible ventrally if present. Occipital surface essentially in vertical plane. Posttemporal fossa well developed; opisthotic sometimes appears in paroccipital bar. Quadrate usually slightly behind level of occipital condyles. Vertebrae neorhachitomous, with reduced pleurocentra, intercentra forming incomplete rings.

Rhinesuchidae. Facial region not abbreviate. Opisthotic appears in paroccipital process. *Rhinesuchus,* M.-U. Perm., S. Afr., ?E. Afr.; ?*Rhinesuchoides,* M. Perm. S. Afr.

Lydekkerinidae. Facial region more or less shortened, opisthotic absent from paroccipital process. *Lydekkerina, Putterillia, Broomulus,* L. Trias. S. Afr.

Uranocentrodontidae. Facial region not abbreviate, Opisthotic absent from paroccipital process. *Uranocentrodon*

U. Perm.-L. Trias, S. Afr.; *Laccocephalus* L. Trias. S. Afr.

?*Sclerothoracidae*. Skull very short and broad. Orbits, external nares and choanae situated far in from skull margins. Cultriform process of parasphenoid very broad. *Sclerothorax*, L. Trias. Eu.; ?*Boreosaurus*, L. Trias. Spitzbergen.

Superfamily Capitosauroidea. Skull, particularly facial region, moderately elongate, snout usually rather slender but external nares lateral in position. Otic notch of normal size, but may be partially or entirely closed by elongate tabular. Skull not greatly depressed. Interpterygoid vacuities somewhat more enlarged than in last superfamily; ectopterygoid elongate, pterygoid in contact with posterior process of palatine medial to the last-named element. Basicranial region and cultriform process of parasphenoid somewhat more flattened than in the rhinesuchoids, the cultriform process not greatly expanded. Parasphenoid-pterygoid contact moderately elongate; exoccipital-pterygoid contact present but not usually visible ventrally. Occipital surface essentially in vertical plane; posttemporal fossae well developed. Quadrate usually slightly posterior to or on level of occipital condyles. Vertebrae almost always neorhachitomous with reduced and usually unossified pleurocentra, intercentra usually incomplete rings. (*Cyclotosaurus* exceptional and resembling brachyopoids in several particulars.)

Benthosuchidae. Primitive capitosauroids. Jaw articulation somewhat behind level of skull condyles. Frontal does not enter orbital rim. External nares not close to tip of snout. Epipterygoid columella not expanded. *Wetlugasaurus*, L. Trias. Russia, E. Greenland, ?S. Afr., ?E. Afr.; *Benthosuchus*, *Volgasaurus*, *Volgasuchus*, L. Trias. Russia; *Sassenisaurus*, L. Trias. Spitzbergen; *Gondwanosaurus*, ?U. Perm. India; *Pachygonia*, L. Trias. India; "*Bothriceps*," U. Perm. Australia.

Capitosauridae. Advanced forms. Jaw articulation about on level of skull condyles. Frontal enters orbital margin. External nares close to tip of snout. Epipterygoid columella expanded. *Parotosaurus*, L. Trias. Eu., Spitzbergen, Russia, S. Afr., Aus.; *Capitosaurus*, U. Trias. Eu.; *Cyclotosaurus*, U. Trias. Eu., ?Spitzbergen, Aus.; *Stenotosaurus*, L. Trias. Eu.; *Stanocephalosaurus*, M.

Trias.(?) N. A.; ?*Kestrosaurus*, L. Trias. S. Afr.; *Mastodonsaurus*, L.-U. Trias. Eu.

Superfamily Brachyopoidea. Facial region of skull short and typically much broadened. External nares not widely separated. Otic notch small or absent. Skull tends to be greatly flattened. Palatal vacuities large, pterygoid generally not reaching forward to palatine. Entire basicranial region and cultriform process of parasphenoid broad and flattened. Pterygoid has greatly elongated contact with parasphenoid and exoccipital, the latter contact usually broadly visible ventrally. Occipital surface slanting so that condyles are well posterior to the posterior margin of the skull table. Opisthotic usually excluded from paroccipital process. Posttemporal fossae reduced. Quadrate anterior to level of condyles. Stereospondylous vertebrae: pleurocentra absent; intercentra form complete cylinders. Clavicle expanded dorsally.

Brachyopidae. Face moderately short, post-orbital region of fairly normal proportions, width posteriorly about equal to skull length. Otic notch much reduced in size. Posttemporal fossa small. ?Vertebrae apparently thin perforated discs. *Bothriceps*, L. Trias. Australia; *Brachyops*, L. Trias. India; *Batrachosuchus*, L. Trias. S. Afr.; *Tungussogyrinus*, ?L. Trias. Siberia; *Pelorocephalus*, M. Trias. Argentina.

Plagiosauridae. Skull as a whole excessively short and broad; breadth exceeds length. Otic notch eliminated. Posttemporal fossa reduced to foramen. Intercentra elongate imperforate cylinders. *Plagiosternum*, *Plagiosuchus*, M.-U. Trias. Eu.; *Gerrothorax*, *Plagiosaurus*, U. Trias. Eu.

Metoposauridae. Face short, but post-orbital region of skull greatly elongated, and hence skull as a whole of normal outlines. Otic notch present but small. Ectopterygoid elongated. Posttemporal fossa small. Vertebrae when completely ossified short but complete discs. *Metoposaurus*, U. Trias. Eu.; *Buettneria*, *Anaschisma* [*Koskinonodon*, *Borborophagus*, *Kalamoiketor*], *Dictyocephalus*, *Eupelor*, ?*Calamops*, U. Trias, N. A.; three genera from U. Trias. India (Huene).

ORDER ANTHRACOSAURIA

Pleurocentra form complete discs enclosing notochord; intercentra variable but of small size. Skull usually high and narrow. Tabular large and in contact with parietal. Palate closed or vacuities, at the most, small; the pterygoids usually meet in midline. Vomers narrow, choanae anteriorly placed and close together. Basipterygoid attachment always movable. Occipital condyle single. Braincase open laterally in laterosphenoid region. Both otic elements well ossified; exoccipital does not extend forward of vagus foramen. ?Five digits in manus.

Suborder Embolomeri. Neural arches of normal type. Intercentra complete discs, in later forms at least; ?primitively crescentic. Skull at least moderately elongate in facial region. Otic notch slit-like, cheek loosely attached to skull table. Tabulars horned. Little development of lateral flange on pterygoid. Quadrate well behind level of occipital condyle. Posterior stem on clavicle short if present. Iliac blade not expanded posteriorly. Posttemporal fossae small.

Anthracosauridae. Cheek region expanded. Jaw articulation far behind level of occipital condyle. *Crassigyrinus*, U. Miss. Scotland; *Anthracosaurus*, L. Penn. Scotland.

Palaeogyrinidae. Skull of normal shape. Postcranial skeleton unknown. *Palaeogyrinus*, L. Penn. Scotland.

Pholidogasteridae. Long-bodied embolomeres. Facial region slightly elongated and somewhat narrow. ?Intercentra not complete discs. *Pholidogaster*, ?*Papposaurus*, U. Miss. Scotland.

Cricotidae. Long-snouted, long-bodied. Intercentra fully formed. *Pholiderpeton*, L.?-M. Penn. Gt. Britain; *Calligenethlon* Penn. N. A.; *Pteroplax*, Penn. England; *Ichthyerpeton*, Penn. Ireland; *Spondylerpeton*, *Cricotus*, U. Penn. N. A.; ?*Nummulosaurus*, U. Penn. Bohemia; *Memonomenos*, ?U. Penn.-L. Perm. Bohemia; *Archeria*, *Eobaphetes*, L. Perm. N. A.

Incertae sedis: *Eosaurus*, Penn. N. A.

Suborder Seymouriamorpha. Dorsal neural arches expanded, swollen: zygapophyses widely separated, with articular faces in horizontal plane. Intercentra persistently crescentic. Skull relatively short. Otic notch typically large and rounded, cheek firmly attached to skull table. Tabulars without horns. Lateral flange of pterygoid well developed. Quadrate on a level with or anterior to occipital

condyle. Long posterior stem on clavicle. Iliac blade typically expanded posteriorly.

?*Diplovertebrontidae.* Intercentra nearly complete discs. Otic notch region as in embolomeres. Face relatively long. Ilium as in embolomeres. *Diplovertebron,* U. Penn. Bohemia.

Discosauriscidae. Intercentra large, but not as highly developed as in last. Skull short. *Discosauriscus,* L. Perm. Germany, ?Russia.

Seymouriidae. Skull not greatly shortened. Intercentra large, but incompletely ossified. *Seymouria,* L. Perm. N. A.; *Rhinosaurus,* L. Perm. Russia.

Kotlassiidae. Skull broad and flat. Palatal teeth in row on palatine and ectopterygoid. Intercentra much reduced. *Phaiherpeton,* L. Perm. Bohemia, Germany; *Kotlassia,* U. Perm. Russia.

STRATIGRAPHIC OCCURRENCE

DEVONIAN

From the fact that in the early Mississippian amphibians of very diverse type had already developed, it is obvious that the origin of the class must have occurred at a time well back in the Devonian. However, there are but two possible records of amphibian skeletal materials in deposits of that period.

In the present review the skull roof specimen described by Westoll as *Elpistostege* is provisionally assigned to the ichthyostegid group of labyrinthodonts. This specimen comes from the famous fish deposits of the Hugh Miller cliff, located between the villages of Fleurant and Miguasha, Quebec, on the south side of the Gaspé peninsula and fronting on the Baie des Chaleurs near "Scaumenac" Bay. The fish fauna has as its three common forms the antiarch *Bothriolepis,* the crossopterygian *Eusthenopteron* and the lungfish *Scaumenacia.* The first two of these forms are known from European deposits; their presence there has aided us in fixing the horizon of the Scaumenac deposits (Westoll 1937, pp. 520–523; cf. Jarvik 1937, pp. 120–121). They appear to be situated stratigraphically in the lower half of the

Upper Devonian and, apparently, at the very base of that subdivision; the flora shows Middle Devonian affinities. The fauna and flora of the Scaumenac locality are definitely indicative of fresh water conditions. Many thousands of specimens of fish have been collected there; it is interesting to speculate as to the ecological conditions which prevailed there, conditions such that in all this material tetrapods or prototetrapods are represented by only one incomplete skull roof.

The second locality which may be of Devonian age lies on Mt. Celsius in East Greenland. Here, in loose material, thought to come from an upper red sandstone layer which contains numerous remains of the antiarch *Remigolepis*, were found the remains of the ichthyostegids described by Säve-Söderbergh (1932). These beds occur at the summit of a series of Devonian deposits, and are believed by this author (1932a) to be of late Devonian age. Westoll (1940) suggests that they may actually be early Mississippian rather than Devonian. Even so, they are surely older than the earliest Scottish fossiliferous beds and are thus definitely the oldest deposits containing unquestioned amphibian remains.

MISSISSIPPIAN

Most of the known Carboniferous amphibians are from deposits of the Coal Measures of late Carboniferous times. Perhaps due to the fact that most European workers do not distinguish between Mississippian and Pennsylvanian, it was hardly realized that certain amphibian finds were from early Carboniferous horizons until attention was called to this subject by Watson (1926, 1929). All described Mississippian, or Lower Carboniferous, amphibians are from Scotland. In that country the Lower Carboniferous rocks include: (1) the Calciferous sandstone series and (2) the Carboniferous limestone series (in the Scottish use of that term), above which the Roslin sandstone forms the transition to the Upper Carboniferous. The lower portion of the Calciferous sandstone series, essentially equivalent to the Tournaisian of the European continent, includes the cementstone group and volcanics, perhaps 1500 feet in thickness; no amphibians are reported. The upper part of the Calciferous sandstone series consists of 3500–4500 feet of the oil shale group, early Visean in age. Here a few amphibians are found. Watson (1929, p. 244) noted the presence of a lepospondylous form in the Curly Shale limestone, and an undescribed lepospondyl in the Harvard collections noted by

Stock (1882) is from the still earlier Wardie limestone at the very base of the oil shale group. Of present importance is the discovery in the Burdiehouse limestone of a single labyrinthodont, *Otocratia*. The Burdiehouse limestone lies approximately in the middle of the oil shale deposits and slightly below the middle of the Mississippian of Scotland. *Otocratia* is thus the oldest of known European labyrinthodonts and the world's oldest except for the possible Devonian forms already mentioned. It is perhaps significant that it appears to be closely related to these earlier types, suggesting that the Ichthyostegalia, although perhaps not ancestral to other labyrinthodonts, were the first group of labyrinthodonts to become widespread and common.

There are no labyrinthodonts reported from the upper portion of the oil shale group. The succeeding Carboniferous limestone series, two to three thousand feet in thickness, is Namurian in age, and generally divided into lower and upper limestone groups, between which is the limestone coal group or Edge Coals, containing several coal seams worked in eastern Scotland. Several labyrinthodonts have been described from the limestone series. The Gilmerton Ironstone lies close to the base of the series. Here were found the skeleton of *Pholidogaster pisciformis*, a skull attributed by Watson to this early anthracosaur, the oldest loxommid, *L. allmannii*, and *Crassigyrinus*, a second anthracosaur. Somewhat higher in the Edge Coal group is the No. 2 Ironstone of Loanhead, from which were obtained the skulls of *Spathiocephalus* and the *Papposaurus* femur.

Apart from Scotland, Mississippian amphibians were unknown before the report of a discovery of vertebrate remains in the Mississippian of West Virginia by the writer (Romer 1941a). The discovery was made in the Hinton shales of the Mauch Chunk group. These shales are near the top of the Mississippian sequence in that region and are believed to be of Lower Namurian age, roughly equivalent in time to the fossil localities of the Scotch Carboniferous limestone series. Unfortunately war conditions have delayed the preparation of this material, which is of a fragmentary nature, but clearly shows the presence of labyrinthodonts; part, at least, of the material is that of an embolomere.

The Mississippian fauna listed is a sparse one. It shows, however, the definite presence of three major groups: the ichthyostegals, the loxommids and primitive anthracosaurs. There are as yet, however, no definite indications of the more characteristic rhachitomous temnospondyls which were to become abundant in the Pennsylvanian.

PENNSYLVANIAN

The Pennsylvanian sequence is best considered from the point of view of the succession of floras. The Upper Carboniferous includes three floral stages: the Upper Namurian at the base; the Westphalian, covering most of the typical Coal Measures; and a short period at the end of the Pennsylvanian alloted to the Stephanian flora, transitional to the Autunian which marks the beginning of the Permian.

Until late in the period most known finds are from the British Isles and hence the succession here must be made with the local terminology in mind. In Great Britain the lowest component in the stratigraphic sequence is the Millstone Grit. This is followed by the Coal Measures, customarily divided into lower, middle and upper divisions, the boundaries between which are vague and apparently not coincident in the various fields. Kidston has used the local terminology for the British floral succession. This consists of the Lanarkian, roughly equivalent to the Upper Namurian; Yorkian (formerly Westphalian in Kidston's usage), equivalent to the lower Westphalian horizons; Staffordian, roughly late Westphalian; and Radstockian, equivalent to the very end of the Westphalian and (probably) early Stephanian (the late Stephanian is unknown in Great Britain).

For the earliest Pennsylvanian (Lanarkian) vertebrates, Scotland continues to be the locality of greatest interest. In eastern Fifeshire there lie above the Roslin sandstone (essentially equivalent to the Millstone Grit) coal deposits with the Lanarkian flora. In one of the parrot coals at Pirnie have been found skulls of the primitive anthracosaur *Palaeogyrinus* and the loxommids *Megalocephalus* and *Baphetes*. Also from Fifeshire is an ilium of the embolomere type. From the Airdrie region of the central coal fields particularly from Chapelhall and Quarter, near Hamilton, has come a variety of labyrinthodont types. Most are from the Black Band Ironstone. These include the type (and only known) specimen of *Anthracosaurus*; a skull attributed by Watson to *Pholiderpeton*; embolomerous vertebrae presumably belonging to one of these two; and a variety of loxommids — *Loxomma*, *Baphetes* and *Megalocephalus*.

Early Pennsylvanian in date, and perhaps late Lanarkian, is the Colne, Lancashire, locality from which comes *Eugyrinus wildi*, which we have considered as the oldest known rhachitome in the customary sense of that term. Stratigraphically its site is the roof of the Bullion Coal of the Burney coal field, in the Mountain Mine horizon.

TABLE OF DEVONIAN AND CARBONIFEROUS LABYRINTHODONT OCCURRENCES

	Stages	*Europe*	*North America*
PENNSYLVANIAN	STEPHANIAN	Kounova (Bohemia); Commentry (France); (late Stephanian) Nýřany, Třemošná (Bohemia) (early Stephanian)	Danville (Ill.); Conemaugh, Monongahela, L. Dunkard (Pa., W. Va., Ohio)
	WESTPHALIAN	(Staffordian, Radstockian of England—barren) Typical English Coal Measures (Yorkian) of Newsham; Bradford (Yorkshire); Staffordshire; Shropshire; Scottish central coalfield; Jarrow (Ireland)	Late Westphalian of Linton (Ohio); Cannelton (Pa.); Mazon Cr. (Ill.); Paris shale (Ark.); Stellarton (N. S.) Typical Westphalian of Joggins (N. S.) (U. Pottsville—barren)
	U. NAMURIAN = LANARKIAN	Lanarkian of Pirnie (Fifeshire); Airdrie (Scottish central coalfield); Colne (Lancs.) in Mountain Mine horizon (Millstone grit—barren)	(L. Pottsville—barren)
MISSISSIPPIAN	L. NAMURIAN = U. VISEAN	Lonehead #2 and Gilmerton Ironstones of Edge coals of Carboniferous ls. series (Midlothian coalfield, Scotland)	Hinton shale of upper part of Mauch Chunk group (W. Va.)
	L. VISEAN = U. DINANTIAN	Burdiehouse ls. of oil shale group = upper part of calciferous ss. series (S. E. Scotland)	
	TOURNAISIAN = L. DINANTIAN	(lower part of calciferous ss. series = cementstone group + volcanics of Scotland—barren)	
DEVONIAN	FAMENNIAN = SENECAN		*Remigolepis* beds (E. Greenland)
	FRASNIAN = CHAUTAUQUAN		Fleurant (Que.)

By the end of the Namurian-Lanarkian, we thus have established all the major labyrinthodont groups characteristic of the typical Coal Measures — ichthyostegals, loxommids, embolomeres, and finally, the oldest of the more typical rhachitomous temnospondyls.

Succeeding the Lanarkian-Namurian horizons in England are the Yorkian or typical Westphalian strata which constitute much of the Coal Measures of Great Britain. A variety of labyrinthodonts has been reported from a variety of localities.

Most prolific of fossiliferous deposits is that associated with the Lower Main Seam of Newsham, Northumberland; this may be fairly early Yorkian in age. Large collections made here by Atthey and other early workers are mainly to be found in the Hancock Museum at Newcastle. All the identifiable labyrinthodont material belongs to two forms: the loxommid *Megalocephalus* and the typical embolomere *Pteroplax*. The same genera are also known from other British coalfields: *Pteroplax* is reported by Watson from the Rag Mine Ironstone of Fenton, Staffordshire; *Megalocephalus* from this last locality, from the Chalky Mine Ironstone of the same county, the Blue Flats Ironstone of Shropshire (Dawley, Coalbrookdale), and the Palace Craig Ironstone of Canboe in the Scottish central Coal Field. A further labyrinthodont from the English Coal Measures is the type skeleton of *Pholiderpeton* from the Blackbed Coal (Upper Yorkian or Lower Staffordian) of Toftshaw, near Bradford, Yorkshire — an embolomere seemingly close to *Pteroplax*.

Unless the last be post-Yorkian, there are no Pennsylvanian labyrinthodonts in the later Carboniferous horizons of Britain — Staffordian or Radstockian. The only other European locality in the typical Coal Measures short of the Stephanian is that at Jarrow Colliery near Kilkenny in the Leinster coalfield of Ireland. I am not aware of any recent work which gives any close correlation of the Leinster field with those of England, but presumably the Jarrow beds are to be correlated with some phase of the Westphalian. Huxley early described certain amphibians from this mine; others have never been adequately described. *Ichthyerpeton* is the skeleton of an animal which appears to be a small embolomere, and much larger specimens have been mentioned in the literature; *Erpetocephalus* is probably a primitive rhachitome comparable to *Pteroplax*.

For the latter part of the Pennsylvanian — late Westphalian stages and the Stephanian — we leave the British Isles, from which almost all the known remains of the earlier Carboniferous have been derived, to turn to two other areas in which the major story of verte-

brate life is continued through not only the late Pennsylvanian but the early Permian as well — North America and central Europe.

In North America (cf. Romer 1935, pp. 1627–1642 in part) the Pottsville, forming the lower part of the Pennsylvanian, is barren of vertebrate remains. However the Joggins deposits of Nova Scotia are of relatively early Pennsylvanian age (Westphalian B, Bell 1944); they appear to be roughly contemporaneous with the typical English Coal Measures. Notable are the erect trees, described by Dawson in numerous publications (1863, 1882, etc.), within which were entrapped small amphibians of various sorts. Most of the remains consist of the primitive rhachitome *Dendrerpeton* and forms closely allied to if not identical with it; there is also an embolomere, *Calligenethlon*. From the Joggins, but from other horizons than that of the "productive tree stumps," have come the *Eosaurus* vertebrae and a jaw fragment, *"Baphetes" minor*.

Apart from this Nova Scotia citation all American Pennsylvanian localities are definitely later in date than those of the British Isles. In the United States the oldest of Pennsylvanian amphibians come from a series of sites which are in the general level of the late Westphalian — zones C and D of the continental European floral series, zones G-H-I of the English system (cf. Westoll 1944, pp. 8–9). Minor localities include the Paris shale of northwestern Arkansas, from which comes the ?rhachitomous femur named *Arkanserpeton*, and Cannelton, Pa., where a cannel coal has preserved a number of small and, in part at least, larval amphibians.

Of greater interest is the famous nodule bed in the region of Mazon Creek, Illinois (Moodie 1916, pp. 12–15, etc.). Most of the nodules contain plant remains; one in 100,000, it is estimated, contains an amphibian. About a dozen amphibians have been found in a century of collecting. These include the embolomerous vertebrae named *Spondylerpeton*; three specimens of the presumed ancestral anurans *Amphibamus* and *Miobatrachus*; and a number of small and presumably larval labyrinthodonts.

Most important of American Pennsylvanian localities is that at Linton, Ohio (Case 1917; Moodie 1916, pp. 17–19, etc.). From a limited area in a mine worked here somewhat after the middle of the last century, an impure cannel, but 6 inches thick, produced a very considerable amphibian fauna. The horizon is that of the upper Freeport coal at the top of the Allegheny, the age latest Westphalian if not earliest Stephanian. Labyrinthodonts present include the ichthyostegals *Colosteus* and *Erpetocephalus*, the loxommid *Macrerpe-*

ton, the primitive rhachitomes *Leptophractus*, *Pelion* and *Saurerpeton*, the more typical rhachitomes *Mytaras*, *Platyrhinops*, *Mordex* and *Stegops*, and the seymouriamorphs or reptiles *Tuditanus* [*Eosauravus*] and *Eusauropleura*. It is noteworthy that (contrary to my earlier belief) there are no definite indications of the presence of embolomeres.

The Stellarton group of the Pictou coalfield is correlated by Bell (1940) with Westphalian C. In the Albion formation of these deposits there were early discovered the skull of *Baphetes planiceps* and an embolomere pelvis.

Several regions in the Ohio River basin have yielded amphibians of Stephanian age. A small bone pocket west of Danville, Illinois, was thought by Cope to be of Permian age, but is now known to be stratigraphically equivalent to some point in the Lower Conemaugh (Romer 1935, pp. 1635–1636). Much of the material is that of a pelycosaur, but the type vertebrae of *Cricotus* (*s. s.*) are from Danville. From the Conemaugh itself, in western Pennsylvania, Case (1908) reported *Eryops*-like vertebrae, and a "*Branchiosaurus*" skeleton has been described (Romer 1939a). In addition Burke and others have collected various amphibian remains, as yet undescribed, from the Conemaugh, Monongahela and "Dunkard" in the Pittsburgh region.

European late Pennsylvanian finds are (except for a "branchiosaur", *Protriton fayoli*, from an Autun basin locality just below the base of the Permian) confined to the Stephanian of Bohemia. Here the major locality is the famous "Gaskohle" of Nýřany (Nyran, Nürschan) of western Bohemia, the fauna of which is described by Fritsch in his famous monograph (1901), and has been recently reviewed by Steen (1938). The horizon is, like that of Linton, Ohio, very close to the Westphalian-Stephanian boundary, and is considered by many authors to be late Westphalian rather than early Stephanian. It is certainly almost contemporaneous with Linton, and the two faunas show many comparable features. Labyrinthodonts include *Loxomma*, the primitive rhachitomes *Gaudrya* and *Cochleosaurus*, the more advanced rhachitomes *Potamochoston*, the seymouriamorph *Diplovertebron*, and *Solenodonsaurus* (perhaps reptilian). Třemošná, another Gaskohle locality in the same basin, has produced the embolomere caudal vertebrae named *Nummulosaurus*.

A much later Stephanian locality — one which, indeed, is very close to the Permian boundary — is the "Gaskohle" of Kounova, of of which the fauna has been recently reviewed by the writer (1945). The fragmentary labyrinthodont remains appear to be those of two

rhachitomes — *Onchiodon* and *Dawsonia* — and an embolomere, referred to *Memonomenos*.

These late Pennsylvanian faunas of North America and Bohemia show certain contrasts with those of the typical Coal Measures. The primitive Carboniferous groups of ichthyostegals and loxommids persist, as do the embolomeres, but the latter are reported relatively rarely. On the other hand, rhachitomes, rare earlier, are an important faunal element, including a number of primitive forms and, particularly in Stephanian deposits, more typical forms comparable with those of the Autunian. A notable new series of faunal elements includes a number of forms — all poorly known — which are either seymouriamorphs allied to the reptiles or may be in part actually primitive cotylosaurs.

PERMIAN

The vertebrates of the early Permian are best represented in the North American redbeds, particularly those of Texas. The stratigraphy of the Texas beds has been discussed repeatedly (see, for example, Romer 1935; Romer and Price 1940, pp. 23–31). They are included in the Wichita and Clear Fork groups. The former is currently held to include, in ascending order, the Pueblo, Moran, Putnam, Admiral, Belle Plains, Clyde and Lueders formations. In the Clear Fork only the lowest formation — the Arroyo — contains vertebrates; higher Permian levels are completely barren. Recent (and still unpublished) palaeobotanical studies by Reid (cf. King 1942) indicate that the *Callipteris* flora, diagnostic of the beginning of the Permian, appears at the base of the Wichita. The entire sequence includes only a limited part of the early Permian.

A very considerable number of labyrinthodonts have been found in these deposits. They include numerous rhachitomes — *Edops*, *Trimerorhachis*, *?Chenoprosopus*, *Eryops*, *Caeops*, *Alegeinosaurus*, *Broiliellus*, *Dissorophus*, *Aspidosaurus*, *Trematops*, *Acheloma*, *Parioxys*, *Zatrachys* — and in addition the embolomere *Archeria*, and *Seymouria*. *Eryops* and *Cricotus* have also been found in a northern continuation of these beds in Oklahoma, and the embolomere *Eobaphetes* is believed to come from the northern part of this same region at the level of the lower Wichita. Certain genera are known only from limited horizons — notably, most of the dissorophids are confined to the Clear Fork. But in many cases this seemingly limited vertical distribution is due only to accidents of collecting, and, for example, *Seymouria*, *Trematops*

and *Acheloma*, once thought to be confined to the Clear Fork, are now known from the Wichita as well. There are, however, certain forms found in the lower beds which do not appear in higher ones. *Edops*, for example, is present — and is locally abundant — in the Pueblo and Moran, but is not found at higher levels. *Archeria* is characteristic of and frequently abundant in the Wichita, but absolutely unknown in the Clear Fork.[1] These two forms are presumably archaic remnants of the Pennsylvanian fauna of primitive rhachitomes and embolomeres. Loxommids and ichthyostegals are unknown. *Seymouria* represents the Seymouriamorpha, which presumably appeared in the late Pennsylvanian. Except for the last three genera all the members of the fauna are rhachitomes and — except for the precociously flat-skulled *Trimerorhachis* — typical eryopsoid members of the temnospondyl assemblage, here at the peak of their career.

In the New Mexican redbeds, roughly equivalent, it would seem, to the lower Wichita, the known fauna is a very limited one — *Eryops*; *Platyhystrix*, closely related to *Zatrachys*; the dissorophid *Broiliellus*; the long-skulled rhachitome *Chenoprosopus*. Curiously, although *Archeria* flourished at this time in Texas, embolomeres are absent in this nearby (although geographically distinct) region.

The European fauna of the early Permian is best known from Central Europe, where the successive Cuseler and Lebach stages of the Rotliegende and its equivalents have furnished vertebrates at a large number of localities. Case (1926) has summarized much of the data on these deposits. A smaller number of finds have been made in France and in England.

There is no general agreement in many cases as to the Lebach or Cuseler age of the deposits concerned; we shall not attempt to distinguish between them, but will merely list notable localities and areas in, roughly, a west-to-east order.

In Great Britain Permian deposits are scanty, and the only Permian amphibian is the skull of *Dasyceps* from red beds, apparently of Cuseler age, at Kenilworth in the Warwick region.

In France, labyrinthodonts are known only from the Autun coal basin. The earlier deposits of the basin are Stephanian, but most of the amphibian remains are from the higher, Permian, beds which contain the characteristic Autunian flora of early Permian age. All known labyrinthodont remains belong to the eryopsid *Actinodon* or to "branchiosaur" larvae.

[1]But see the earlier discussion of *Archeria*.

To the east, much of the Saar-Palatinate region shows exposures of the Lebach stage. In the famous nodule beds of the Saar basin, the long-snouted rhachitome *Archegosaurus* is very common, and in addition there is a shorter-faced eryopsid referred to *Actinodon*. From the Palatinate have come a number of specimens of the related eryopsid *Sclerocephalus* as well as "branchiosaurs" which may be larvae of this genus. East of the Palatinate abundant "branchiosaurs" have been found at Odernheim (Rheinhessen). Much farther to the east, Permian shales (Goldlauter beds, Lebach horizon) at Friedrichroda in Thuringia have yielded good material of "branchiosaurs".

Most famous of European Permian vertebrate localities is that of Niederhässlich or the Plauen'sche Grund, in deposits of Lebach age in the small Dohlen coal basin on the outskirts of Dresden. The shales here have yielded a large amount of amphibian material. Most specimens are typical "branchiosaurs", presumably larvae of the eryopsid *Onchiodon*, of which larger individuals are also represented. Other labyrinthodonts, less abundant, are the zatrachyid *Acanthostoma* and the seymouriamorphs *Discosauriscus* and *Phaiherpeton*.

In the Sudetic basins among the mountains on the Bohemian-Silesian borders are Lower Permian deposits containing amphibians as well as other lower vertebrates. From Klein Neundorf in the North Sudetic basin near Löwenberg, Silesia, comes the unique type of the eryopsid *Ostcophorus*. Farther to the southeast, in the middle Sudetic basin, shales at Olivětín (Olberg) and Ruprechtice (Ruppersdorf) near Broumov (Braunau) in eastern Bohemia have yielded remains of *Lusor*, *Phaiherpeton* and *Chelydosaurus*, and larvae and problematical forms probably to be assigned to these three types. A *Phaiherpeton* is also reported from Horní Kulná near Kunčice, west of this area.

Still farther to the south, a long strip of Permian deposits in the "Boskovice furrow" in western Moravia has produced an abundant fish fauna, but of tetrapods it exhibits only numerous specimens of the small seymouriamorph *Phaiherpeton*. At Košťálov, near Pilsen, beds which appear to lie at the very base of the Permian have yielded the skull of *Memonomenos*, apparently a late-surviving embolomere.

The early Permian fauna in Europe, just reviewed, shows a general similarity in certain regards to that of the American redbeds. In Europe as in America, this is the time of dominance of typical rhachitomes. The greater part of the known material appears to pertain to genera closely related to the common American genus *Eryops*; *Dasyceps*, *Acanthostoma* and *Archegosaurus* represent two further rhachitome

families. Present also, as in America, are seymouriamorphs and a final embolomere representative. There are notable differences from the American fauna. We find, for example, no representatives of the stout-limbed eryopsoids of the dissorophid or trematopsid groups; and a great part of the material consists of larval specimens, almost unknown in America. These differences are, I think, to be correlated in great measure with differences in the nature of the deposits. Those of America are clays suitable for the preservation of the bones of large animals as three-dimensional structures; and shales suitable for the preservation of small animals and delicate larvae are rare. The reverse situation holds in Europe with consequent differences in the nature of the preserved fauna.

Probably of early Permian age are the oldest amphibian remains at present known from any region other than Europe or North America. The Kuling system of Kashmir contains near its base fossiliferous shales with *Gangamopteris* and fishes of early Permian aspect. Amphibians are reported from Khunmu and Zewan; they include a form comparable to *Archegosaurus* at the former locality and two individuals of *Lysipterygium*, a rather primitive rhachitome, at the latter.

Characteristic of the early Permian is the disappearance of ichthyostegids and loxommids, the extinction in the earliest Permian of the embolomeres, survival of seymouriamorphs, and dominance of eryopsoids, these last marking the height of temnospondyl evolution toward terrestrial existence.

Beyond the early Permian deposits represented by the American Clear Fork and the lower portions of the European Rothliegende, the geographical locale of amphibian-bearing deposits shifts markedly. The later American Permian beds are absolutely barren; and the later Permian of Europe has but few vertebrates of any sort and no amphibians. Instead we find the Ural region of Russia and the Karroo region of southern Africa as the two centers of interest.

Fossiliferous deposits in Russia begin above the Artinskian, presumably equivalent in general to the upper Wichita and lower Clear Fork of North America, and continue without major break into the Lower Triassic. Recent active exploration by Russian workers has revealed the presence of a number of successive vertebrate faunas which are currently arranged in six zones (Efremov 1937a, pp. 121–126; 1939a; 1940; Mazorovich 1939). The Russian beds cover a vast area along the western slopes of the Urals, west to the middle Volga, and north into the Arctic.

In South Africa the thick but barren Ecca beds are presumably representative of the Lower Permian. Succeeding them are the fossiliferous continental deposits of the Beaufort series, which carry the vertebrate story up into the Lower Triassic. Above the Beaufort, the Stormberg Series continues the continental record through the remainder of the Triassic but there are no recorded amphibians in this series. Huene (1925) has summarized the successive Beaufort faunas, six in number, which are named on the basis of characteristic genera.

Huene (1940a) has recently given faunal lists for most of the world's terrestrial vertebrate faunas of the Permian and early Triassic, and Watson (1942, pp. 109–116) has most recently discussed the correlation and geological age of Russian and South African beds.

Oldest of the Russian deposits are those of Zones I-II (Kungurian and Kazanian stages). The two zones are closely related lithologically and faunally, and are difficult to distinguish. It seems probable that their time of deposition followed closely that of the fossiliferous Clear Fork and the Lebach stage. Characteristic of these beds are the dinocephalian reptiles *Rhopalodon* and *Titanophoneus*, similar to South African forms but more primitive and hence presumably older. The beds of these two zones occupy a vast triangular area between Perm, Orenburg (Čkalov) and Kazan, mainly in the basin of the Kama River west of the southern Urals, and include copper deposits worked in the last century.

The amphibian faunas of Zones I-II include: *Zygosaurus*, a surviving dissorophid; *Chalcosaurus*, poorly known but apparently similar to *Trimerorhachis* of Texas; *Melosaurus* and primitive species of *Platyops* — both members of the archegosaurid group; several other rhachitomes as yet undescribed; and several seymouriamorphs — *Discosauriscus*, *Rhinosaurus* and *Lanthanosuchus*. In this late Lower Permian assemblage we appear to see a fauna closely related to and readily derived from that of the earliest Permian of the "Atlantic" region.

With Zone III of the Russian series and the *Tapinocephalus* zone of South Africa, we reach deposits which it is generally agreed are Middle Permian in age. The Russian "Pelycosaur Zone" may be a terminal phase of the Kazan cycle or part of the Tartarian or Chlynovian stage (Urzhum formation). Vertebrates are reported from two main areas, one in the Mesen River valley in the far north, the other in the valley of the Vyatka (there is a small intermediate area on the Suchona River). The amphibian fauna is sparse. Reported are forms comparable to *Melosaurus* and *Zygosaurus* of the lower zones, and a

progressive *Platyops* (*P. watsoni*). This suggests possible isolation at this time and little evolutionary progress in genera.

In South Africa, the lowest fossiliferous beds of the Beaufort Series are those of the *Tapinocephalus* zone, abundantly fossiliferous in the desert Gouph area of central Cape Province. The amphibian fauna includes only two genera — *Rhinesuchus* and a long-faced relative, *Rhinesuchoides*. These are the oldest of the "neorhachitomes". Although the paucity of amphibian remains of Middle Permian age in both Russia and South Africa is disappointing, we at least see in the Karroo the initiation of a progressive development which may have given rise to many of the temnospondyls of the late Permian and Triassic.

The late Permian is represented in Russia by Zone IV, the pareiasaur zone, in the Sarma Formation of the Chlynovian (lower, true Tartarian) stage. The Sarma Formation is widespread in European Russia. It occupies a large area west of that in which Zones I-II are exposed, from Orenburg to the Middle Volga and northeast to Perm; covered by higher beds in the region of the Volga-Dvina divide, the Sarma reappears in the north, to be exposed over much of the Dvina watershed. From sandy lenses near Kotlas in this latter area come materials of pareiasaurs and other forms comparable to those of the Upper Permian of South Africa (*Cisticephalus* zone). Only two amphibians have been described: the neotenous rhachitome *Dvinosaurus* and the last surviving seymouriamorphan, *Kotlassia*.

In South Africa, the Upper Permian is represented by the successive *Endothiodon* and *Cisticephalus* zones, abundantly fossiliferous in large areas of Cape Province in the general region Beaufort West — Murraysburg — Graaf Reinet. As in the *Tapinocephalus* zone, the labyrinthodont record is a disappointing one. There are merely a few specimens of neorhachitomes of the general *Rhinesuchus* type. That genus itself is reported from the *Endothiodon* zone. In the *Cisticephalus* zone is found "*Laccosaurus*," possibly generically identical with *Uranocentrodon* of the Eotriassic, and one specimen from this zone has been assigned to the latter genus.

In the late Permian there is some extension of the area of discovery of amphibian finds in the Old World. In East Africa, a bonebed of Upper Permian age in the Ruhuhu district of Tanganyika has remains of *Rhinesuchus*-like amphibians. In India, it is possible that the Mangali beds containing *Brachyops* are late Permian, although they are here included in the Eotriassic.

In Australia the Newcastle Coal Measures appear to be definitely of Upper Permian age. From them at the Airly mine near Lithgow, N.S.W., came the only specimen of *"Bothriceps" major*, which does not belong to that brachyopid genus, but is seemingly an immature individual of a relatively long-snouted neorhachitome.

It is obvious that our current picture of amphibian development in its Upper Permian stage is an incomplete one. In Russia, we see a lingering primitive rhachitome and the last of the seymouriamorphs; elsewhere, a few progressive neorhachitomes. We know little or nothing, however, of the considerable differentiation of temnospondyls which must have been under way at this time to produce the varied groups found in the Triassic.

TRIASSIC

For the later phases of the Permian, the amphibian record was almost exclusively one from the Karroo of southern Africa and from the continental sediments of eastern Russia. These two series of sediments continue into the early Triassic; beyond this, however, the amphibian record ceases for these areas. Triassic finds, however, are almost worldwide in distribution; fossil amphibians of this age are recorded from every continent, and the deposits of central and western Europe, in which the amphibian record stopped early in the Permian, again enter the picture and play an important role.

The customary standard for consideration of the continental Triassic has been the German section, with its three classic subdivisions — continental Bunter deposits at the bottom, followed by the marine Muschelkalk, and above this the Keuper (in a broad sense), mainly a continental series. This tripartite division, however, appears to represent merely local conditions in which a marine transgression from the south, followed by a later regression of the seas, interrupts the continental sedimentation of central and northern Europe. For the study of amphibian faunas it is perhaps better, in the present rather inadequate state of our knowledge, to consider the Trias as composed of early and late phases, both of which may be further subdivided. In the Lower Triassic or "Eotriassic" (Scythian stage), earlier and later phases may be distinguished (cf. Spath 1934, pp. 25–34), and the Rhaetic may be treated separately as a final Triassic stage following the Keuper.

The Lower Triassic amphibians of central Europe are found, apparently, only in the upper part of the Bunter; the lower portions

TABLE OF PERMIAN AND TRIASSIC LABYRINTHODONT OCCURRENCES

	Stages	*Europe*	*Africa*	*Asia*	*Australia*	*America*
TRIASSIC	RHAETIC	Halberstadt (Thuringia); bonebeds of Germany, Scania				
	NORIAN, CARNIAN	Hauptkeuper of Swabia, Franconia, Thuringia, Lorraine, incl. Stubensss., Schilfss., Lehrbergstufe, Blasensss.; Raibl beds of Alpine Trias; U. Trias of Spitzbergen		Maleri beds (India)	Wianamatta series (N.S.W.)	Newark of eastern U. S.; Chinle, Dockum, Chugwater (Popo Agie) of Ariz., N. Mex., Wyo., Texas
	LADINIAN	Lettenkohle (L. Keuper) of Swabia, Thuringia incl. Gailsdorf, Molsdorf, etc., Lorraine; Keuper of Warwick and West of England				
		U. Muschelkalk of S. Germany (Crailsheim etc.) and Lorraine				?Cacheuta beds (Argentina)
	ANISIAN	L. Muschelkalk (Wellenkalk) of Gogolin (Silesia), Halle, Lorraine	(L. pt. Stormberg series)			
	SCYTHIAN	M.-U. Bunter of Franconia, (Bernburg Anhalt), U. Rhine region (Kappel), Hessen, Thuringia, Helgoland; Spitzbergen (mainly marine fish horizon, *Posidonomya* zone); zone VI of Russian sequence (Gt. Bogdo, Ckalov [Orenburg])	*Cynognathus* zone of Beaufort series (S. Af.); Manda beds (E. Af.)	?Korwuntchan series of Tungus basin (Siberia)	Hawkesbury series (N.S.W.)	Moenkopi, Ariz.
		Russian zone V = Vetlugian stage of Tartarian in Volga, Dvina, Mesen R. valleys, Timan	*Procolophon* and *Lystrosaurus* zones of Beaufort series (S. Af.); Ranohira (Mad.); Ruhuhu upper bed (E. Af.)	?Panchet, Bijori, Mangali beds; *Prionolobus* zone of Salt Range (India)	Narrabeen series (N.S.W.); ?Ross ss. (Hobart, Tasmania)	E. Greenland

TABLE OF PERMIAN AND TRIASSIC LABYRINTHODONT OCCURRENCES CONT.

	Stages	*Europe*	*Africa*	*Asia*	*Australia*	*America*
PERMIAN	THURINGIAN	Russian zone IV (Pareiasaurian) = Sarma fm. of Chlynovian (L. Tartarian) stage, West of Urals, M. Volga, Dvina basin (Kotlas, etc.)	*Cisticephalus* and *Endothiodon* zones of Beaufort series (S. Af.); Ruhuhu lower bed (E. Af.)		Newcastle Coal Measures	
	SAXONIAN	Russian zone III (Pelycosaurian) = Urzhum fm. of Chlynovian (L. Tartarian) stage of Mesen and Vyatka rivers	*Tapinocephalus* zone of Beaufort series (S. Af.)			
		Russian zones II-I (*Titanophoneus*, *Rhopalodon*) = Belebey fm. of Kazanian, Ufa fm. of Kungurian, of Perm-Orenburg-Kazan region	(Ecca)			(U. Clear Fork)
	AUTUNIAN	Lebach and Cuseler stages of Rothliegendes, Warwickshire, Commentry, Saar, (Lebach), Palatinate, Thuringia (Friedrichroda), Niederhässlich (Saxony), N. Sudetic basin, Broumov, Boskovice, etc, (Czechoslovakia) (Barren Artinskian of Russia)		Shales of Kuling system of Kashmir (Khunmu, Zewan)		Wichita and L. Clear Fork (Tex.-Okla.-Kans.), Abo (N. Mex.), Dunkard (Ohio-W. Va.)

(difficult to distinguish from the almost equally barren Zechstein) have no certainly determined amphibian remains. Earlier assemblages are found in other areas — notably South Africa, Russia and East Greenland. These are equivalent to the earlier phases of the Scythian stage of the marine Triassic.

In South Africa the *Lystrosaurus* zone is usually considered as the base of the Triassic. This is a relatively thin zone, but productive both in the south, in northern Cape Province and the adjacent regions of the Orange Free State, and (unlike other horizons) in the north, near Harrismith, O. F. S. The remains of a number of "neorhachitomes", presumably descended from or related to the *Rhinesuchus* group, are present. These include: *Uranocentrodon*, *Lydekkerina*, *Laccocephalus*, *Putterillia* and *Broomulus*. Watson (1942) notes an undescribed form which may belong to the contemporary Russian genus *Wetlugasaurus*. This same author mentions an undescribed skull from an upper Ruhuhu bonebed in East Africa which may be intermediate between *Rhinesuchus* and *Wetlugasaurus*.

Beds in Madagascar (near Ranohira) have produced amphibian remains which have been compared with *Uranocentrodon* and may be "Eotriassic" in age.

Above the *Lystrosaurus* horizon is the thicker *Procolophon* zone, consisting mainly of deposits of more terrestrial type, productive in the Orange River region and adjacent portions of Cape Province. The fauna is a relatively sparse one. Of amphibians, there are no records of the neorhachitomes; the only forms are the persistently primitive rhachitome *Micropholis* and the slender-skulled capitosauroid *Kestrosaurus* which is apparently transitional between the wetlugasaurs and true capitosaurs.

In Russia, Zone V, the *Benthosuchus* Zone of Efremov's classification, is considered to be of earliest Triassic age and in consequence roughly equivalent to the *Lystrosaurus* and *Procolophon* zones of South Africa. This zone includes the variegated beds of the Vetlugian stage of the geologists, the upper part of the Tartarian. These beds cover a great expanse of country, from the region of the Upper Volga and the divide between Volga and Dvina watersheds, far to the northeast through the watersheds of the Dvina and Mesen Rivers to the Timan region. Efremov believes that there was at this time a short period when water was abundant and swamps widespread in this part of Russia. The amphibian fauna is neorhachitomous as was that of South Africa, but the forms described are all variants of a single pattern, that of the long-snouted benthosuchid capitosaurs —

Benthosuchus, *Wetlugasaurus*, *Volgasuchus* and *Volgasaurus* [*Thoösuchus*]. There are no traces of other neorhachitomes or of possible ancestors of the non-capitosaur amphibians of the Triassic.

In East Greenland at Cape Stosch, the Lower Triassic includes, in part of a marine series, the *Anodontophora* beds which have yielded a number of amphibian finds. These deposits, usually called Eotriassic in some sense of that term, are often correlated with the marine Lower Triassic vertebrate-bearing strata of Spitzbergen. They appear, however, to be slightly earlier in age and closer to the Russian beds in certain regards. This conclusion, reached on the basis of the Amphibia, is in agreement with the geological evidence (Spath 1935), which is not decisive, but suggestive of late Lower Scythian age.

Of the amphibians (described by Säve-Söderberg), there are forms identified with *Wetlugasaurus* of the Russian Eotriassic and numerous trematosaur remains, including several species assigned to *Lyrocephalus* but perhaps generically distinct, and *Stoschiosaurus*, incompletely known but probably long-snouted.

A series of deposits in India which are of early Triassic age may be discussed here, although their exact position is uncertain.

The Bijori beds of central India, containing the remains of the benthosuchid neorhachitome *Gondwanosaurus* may be Eotriassic in age; the geological evidence is indeterminate between late Permian and early Triassic.

A number of specimens have been derived from the Panchet beds, also in Central India. These include the genotype of the long-snouted trematosaur *Gonioglyptus*; a jaw fragment (*Glyptognathus*) possibly belonging to the same; *Pachygonia incurvata* and *"Gonioglyptus" huxleyi*, jaw fragments apparently benthosuchid in nature; and vertebrae and jaws of a brachyopoid, presumably *Brachyops*. The type of this last genus is from Mangali beds near Nagpur, also in Central India. Of Lower Scythian age is the *Prionolobus* zone of the Triassic of the Punjab Salt Range marine deposits from which comes the skull of *Gonioglyptus kokeni*.

The Narrabeen series of New South Wales is currently believed to be equivalent to the Lower Bunter. From Gosford, in these beds, come the presumed larval brachyopids described as *Platyceps wilkinsonii*. From the Ross sandsone of Hobart, Tasmania, thought also to be a Lower Bunter equivalent, have come small femora which are either amphibian or cotylosaurian in nature[1].

[1]Lydekker (1890, p. 214) compares them with *Eryops*; David (1932, pp. 74, 76) quotes Watson to the effect that they are captorhinid.

Other beds which may lay claim to Eotriassic age in a rather broader sense are found in Spitzbergen; these will here, however, be considered with more typical Lower Triassic deposits below.

The fauna of the Lower Eotriassic as limited here consists in great measure of neorhachitomes of one sort or another. In South Africa much of the fauna consists of round-snouted forms, readily derivable from the rhinesuchoid pattern and not definitely known elsewhere at this stage (unless *Borcosaurus* of Spitzbergen is of this category). In Russia, on the other hand, the entire known fauna consists of neorhachitomes of another sort — long-skulled genera leading directly, it would seem, into the capitosaurs of typical Triassic horizons. This type of amphibian is also represented in other areas: in Greenland we find the Russian genus *Wetlugasaurus*; in Africa, *Kestrosaurus* is not far distant from the Russian neorhachitomes; *Wetlugasaurus*-like specimens are reported from both South and East Africa; *Gondwanosaurus* and *Pachygonia* of India are apparently benthosuchids. In Greenland the majority of the material is that of a third group — the trematosaurs. Representatives of both long- and short-snouted variants are present in *Stoschiosaurus* and *Lyrocephalus*, respectively. *Gonioglyptus* is a long-snouted Indian trematosaur representative. Brachyopids are present in "Gondwanaland", with *Bothriceps* in India, the "*Platyceps*" larvae in Australia. *Micropholis* of the Karroo is a primitive rhachitomous survivor. The seymouriamorphs, which persisted in Russia throughout the Permian, now appear to be extinct. The Lower Eotriassic includes types possibly ancestral to all the groups of the later Triassic except the metoposaurs — who may, however, be allied in ancestry to the brachyopids.

The more typical Lower Triassic, or Upper Eotriassic, is best represented in central Europe, in the Bunter deposits of the Rhine region and central Germany. As has been said, the Bunter vertebrates are seemingly restricted to the upper part of that group. The best known locality is that in the upper part of the Middle Bunter of Bernburg in Anhalt. Here there have been found numerous skulls of *Trematosaurus brauni* and *Parotosaurus nasutus*. Unique specimens from this site include "*Capitosaurus*" *fronto*, a capitosaur but one certainly distinct from *P. nasutus*, and "*Labyrinthodon*" *ocella*, probably a *Trematosaurus*.

A second important locality is the Upper Bunter "Leichenfeld" of Kappel, near Villingen, Baden, in the Schwarzwald, whence have come numerous remains of *Mastodonsaurus* (*Heptasaurus*) *cappelensis*, closely related to and probably ancestral to the typical *Mastodonsaurus*

of the later Triassic. Several other finds of *Mastodonsaurus*-like amphibians from the Bunter may belong to the same or to closely related forms. These include other Schwarzwald fragmentary amphibian remains reported from the Bunter of Calw and Nagold, Württemberg. Farther afield, we note the peculiar rhachitome *Sclerothorax* from the Bunter of Queck in Hessen, the type of *Trematosaurus fuchsi* from the Middle Bunter of Kahla in Thuringia, and the skull of *Parotosaurus helgolandiae* from a Bunter deposit of uncertain horizon in Helgoland.

Best considered with the Bunter assemblage are specimens from the Lower Muschelkalk: the "*Mentosaurus*" jaw from the Halle region, presumably an early *Mastodonsaurus*, the skull of "*Capitosaurus*" *silesicus* from the Lower Wellenkalk of Gogolin, Upper Silesia, and fragments of capitosaurs (described as "*Cyclotosaurus*") from an equivalent horizon in Lorraine.

In southern Russia typical Lower Triassic beds (Zone VI of Efremov) are present in the Kampil Limestone of Great Bogdo, in the Astrakhan region, where a *Trematosaurus* comparable to that of Bernburg, and "*Capitosaurus*" *bogdoanus* are found, and, to the Northeast, on the Dongus River in the Čkalov (Orenburg) region, where, in variegated clays, a questionable "*Capitosaurus*" is reported.

Quite in contrast with the continental Bunter are Lower Triassic deposits of Scythian age in Spitzbergen (cf. Frebold 1930, for geology). The *Posidonomya* beds are for the most part marine in origin, with numerous invertebrates, and fishes which well may be marine in habitus. Wiman and later writers have described seven genera of amphibians — *Lonchorhynchus* [*Aphaneramma*], *Lyrocephalus*, *Tertrema*, *Peltostega*, *Platystega*, *Boreosaurus*, and *Sassenisaurus*. The last is from a rather higher horizon than the others, and one with less suggestion of marine origin; this and *Boreosaurus* are presumably neorhachitomes. The remaining genera — of which the first two are the most common — are all trematosaurs. Their abundance in this marine deposit, associated with numerous fishes, reasonably suggested to Wiman that we are dealing with a group of specialized fish-eating marine amphibians.

It seems abundantly clear that the *Cynognathus* zone of South Africa is equivalent to much of the Bunter of Germany. This zone is the top of the Beaufort Series, and includes about 2,000 feet of red continental sediments in eastern Cape Province and the southeastern corner of the Orange Free State. This horizon marks the end of the amphibian record in the Karroo System; there is none in

the relatively barren Stormberg Series above this. Most prominent of amphibian finds are a number of typical capitosaurs noted in the discussion of *Parotosaurus*, and originally described as "*Capitosaurus*" and "*Cyclotosaurus*". The trematosaurs are represented by *Trematosuchus*, apparently closely related to *Trematosaurus*, and a poor specimen doubtfully assigned to the latter genus. *Rhytidosteus* and *Microposaurus* (if distinct) are more specialized trematosaurs. *Batrachosuchus* is a well-developed brachyopid.

In Asia, the Korwuntchan (Upper Angaran) Series of Siberia may be of early Triassic age. From these deposits, in the Tungus River basin, comes *Tungussogyrinus*, presumably a larval brachyopid.

The brachyopid *Bothriceps australis* comes from an unknown locality in Australia which is generally assumed to be in the Hawkesbury Series, currently regarded as equivalent to the upper part of the Bunter. From these beds is reported a primitive capitosaur (?*Parotosaurus*).

In North America the Moenkopi beds of the Arizona region appear to cover a considerable part of early Triassic time. The one described form is *Stanocephalosaurus* but Welles (1946) has announced the discovery of several other capitosaurs, a brachyopid, and a long-snouted trematosaur.

We may note here the only known South American labyrinthodont of any age — the brachyopid *Peloroccphalus* from the upper part of the Cacheuta beds of Mendoza Province, Argentina. These deposits are assigned to the Middle Triassic, or even to the lowest Upper Triassic, but the genus is similar to the Old World brachyopids and may reasonably be considered in connection with the early Triassic fauna.

In the typical Lower Triassic deposits described above, we witness the establishment of most of the prominent groups of Triassic amphibians. The capitosaurs are seemingly ubiquitous, and are represented mainly by relatively primitive forms of the *Parotosaurus* type, and early members of the *Mastodonsaurus* phylum. Trematosaurs were abundant, particularly in seemingly marine deposits, in the Lower Triassic, but seem to have disappeared shortly after reaching their climax; perhaps the rise of marine reptiles may have contributed to their downfall. The brachyopids are unknown in Europe, but are characteristic, seemingly, of "Gondwanaland" deposits in Africa, Asia, Australia, and even South America. There are no known members or certain ancestors of the metoposaurs of the later Triassic. There are remnants of the neorhachitomes of the early Eotriassic surviving in Spitzbergen, Europe, and South Africa.

The continental faunas of the latter part of the Triassic are best known from the typical European deposits — the Keuper in a broad sense. We shall here include certain finds from the later Muschelkalk which are obviously part of the Upper Triassic fauna. The Keuper is generally subdivided into three portions, to which the terms Lettenkohle, Haupt- or Gipskeuper, and Rhaetic are generally applied.

The Upper Muschelkalk contains a number of labyrinthodont finds; most of the material comes from a series of bonebeds at Crailsheim in Swabia, presumably at the margin of the retreating Muschelkalk sea, and separated only by a last dolomite layer from the continental Lettenkohle deposits. Here are found fragments of a large labyrinthodont, thought to be *Mastodonsaurus,* and we have here the first appearance of the peculiar short-headed plagiosaurs, already represented by two forms — *Plagiosternum granulosum* and *Plagiosuchus pustuloglomeratus.* A large tooth from the Upper Muschelkalk has been described as *Mastodonsaurus meyeri,* and from the Muschelkalk-Lettenkohle boundary in Baden comes the partial skull of *Cyclotosaurus papilio.* From the Upper Muschelkalk of Lorraine are described fragments of *Mastodonsaurus* (?) and plagiosaurs, perhaps *Plagiosuchus.*

The Lettenkohle, or lower Keuper (s.l.), is rather more fossiliferous; Gailsdorf, in Swabia, which has produced fine remains of *Mastodonsaurus giganteus* is the best known fossil locality. Here also are found plagiosaurs, apparently the same genera as at Crailsheim: *Plagiosternum* sp. and *Plagiosuchus pustuliferus.* Other Lettenkohle finds from Swabia include *Mastodonsaurus acuminatus* from Hoheneck, and *M. giganteus* from Markgröningen. Thuringian deposits have produced various fragmentary Lettenkohle labyrinthodonts, mostly from Molsdorf. A large portion of a skull is ascribed to *Mastodonsaurus acuminatus*; other remains ascribed to *M. giganteus* and *Mastodonsaurus* sp. include typical vertebrae; there are various fragments of plagiosaurs, described as *Plagiosuchus pustuloglomeratus* and *Plagiosternum* sp.; *Trigonosternum* from Koll is an incomplete interclavicle which may be that of *Metoposaurus.*

The Hauptkeuper, or Keuper in a restricted sense, is abundantly fossiliferous. Amphibian remains are most common in Swabia, many from the Stuttgart neighborhood. The Stuttgart Schilfsandstein, low in the Hauptkeuper, has produced, besides a rich reptilian fauna, fine materials of *Metoposaurus diagnosticus, Cyclotosaurus robustus* and fragmentary remains of *Mastodonsaurus* (*M. keuperinus*). Farther north, at Würzburg, a large tooth from the Schilfsandstein is described

as *M. andriani*, and from this formation at Benk in Franconia was described the type of *Capitosaurus arenaceus*.

Somewhat higher in the Stuttgart section than the Schilfsandstein is the Lehrbergstufe, mainly a marine dolomite band, but containing some presumably drifted vertebrates; these include the relatively small *Metoposaurus stuttgartensis* and *Plagiosaurus striopustulatus*. At Ebrach, in Upper Franconia, the Blasensandstein, lying above the Schilfsandstein, has yielded skulls of *Metoposaurus heimi* and *Cyclotosaurus ebrachensis*, and a plagiosaur interclavicle described as *Gerrothorax franconicus*. A prominent late Keuper horizon is that of the presumably deltaic Stubensandstein, with numerous reptilian and amphibian remains which at Pfaffenheim in Swabia include the large skulls known as *Cyclotosaurus mordax* and *C. postumus*, and *Plagiosaurus pulcherrimus*. *Metoposaurus* and *Cyclotosaurus* are reported, on the basis of fragments, from the Keuper of Lorraine.

Farther to the South, in the predominately marine Alpine Trias, "*Mastodonsaurus*" has been reported on the basis of poor and essentially indeterminate fragments from various localities; a skull named *Metoposaurus sanctaecrucis* has been described from the Raibl beds, equivalent to the Middle Keuper, of the South Tyrol.

Fragmentary remains of large labyrinthodonts — most of them consisting of partial jaws — have been described from the Upper Trias of southern England; most of these are from an early Keuper phase. "*Labyrinthodon*" *lavisii* is from Sidmouth; *Cyclotosaurus stantonensis* from Staffordshire; "*Labyrinthodon*" *leptognathus*, *Mastodonsaurus pachygnathus*, and *Diadetognathus varriecnsis* are from Warwickshire. All appear to be capitosaurid in nature, and probably pertain to *Cyclotosaurus* and *Mastodonsaurus*. In the Upper Triassic of Spitzbergen has been found a large intercentrum of capitosaur type, presumably of *Cyclotosaurus*.

In India, late Triassic remains are known from the Maleri stage, mainly from Maleri village in central India (Huene 1940). These are beds of continental type, comparable to those of the Keuper. There are jaw fragments and vertebrae which are apparently brachyopoid, and three metoposaurs. A large plate from deposits at Denwa was named *Mastodonsaurus indicus*, but this assignment is quite uncertain.

In Australia, excellent *Cyclotosaurus* material, as yet undescribed, has been found in the Wianamatta beds, presumably equivalent to the Keuper.

Except for the Moenkopi (Ariz.) materials mentioned above, the American record of amphibians is a blank from a very early stage

in the Permian to the late Triassic — deposits of intervening ages are almost completely barren of vertebrate remains and dominantly marine. In the Upper Triassic, however, continental redbeds comparable to the Keuper are present in both eastern and western North America. In the East such deposits constitute the Newark series of southern New England and a belt along the Piedmont from New Jersey to the Carolinas. Three genera of amphibians have been described. *Dictyocephalus* from North Carolina is a typical metoposaur; *Eupelor* of Pennsylvania is reasonably regarded as a member of this group; *Calamops*, a partial jaw from this last state, is indeterminate but may be a metoposaur. In the Triassic of the West, metoposaur remains are abundant in Wyoming, Texas, New Mexico and Arizona. The beds concerned include the Popo Agie of Wyoming, the Dockum of Texas, the Chinle of Arizona, and New Mexican beds comparable to and not improbably contemporaneous with both of the last two. Five genera have been described: *Anaschisma*, *Buettneria*, *Borborophagus*, *Koskinonodon* and *Kalamoiketor*. All are closely related to one another — and to *Dictyocephalus* — and generic differences are slight if any. It is noteworthy that, despite the abundance of metoposaur remains, there is not as yet the slightest trace of any capitosaur or plagiosaur.

The Rhaetic of central and western Europe shows a trend back toward marine conditions transitional to the typically marine Lias. Most famous of Rhaetic deposits are the various bonebeds, particularly in Württemberg. These contain fragmentary and unidentifiable labyrinthodont remains (E. Huene 1933). In other very late Triassic deposits which may be included in the Rhaetic there are a number of amphibian finds indicating the persistence of the labyrinthodonts (Nilsson 1937, pp. 64–65). Again, most are fragmentary. Impressions in the Rhaetic quartzite of Schötmar, Lippe, were believed by Fraas to have been made by *Cyclotosaurus*; Miall and Huene have listed *Metoposaurus* as present in the Rhaetic of Bristol, but no material has ever been described; capitosaurid intercentra and associated teeth from an early Rhaetic level at Halberstadt in the Harz region were described by Jaekel as *Hercynosaurus carinidens*; and *Gerrothorax rhaeticus* is from the Rhaetic of Scania. The last is a well founded plagiosaur; the others do little more than indicate that capitosaurs, at least, were present to the end of the European Triassic.

In the Upper Triassic, as reviewed, the labyrinthodonts are a restricted group. The older rhachitomes and neorhachitomes have disappeared; the trematosaurs, abundant in the Lower Triassic, have

likewise vanished. Capitosaurs are represented by large end-forms: *Cyclotosaurus* and larger specimens of *Mastodonsaurus*. The metoposaurs make their only appearance at this time; we have noted that there are no known Lower Triassic forms antecedent to them. *Metoposaurus* is the European representative; *Buettneria* and *Anaschisma* are among the American genera of a slightly different type; three forms are reported from India; none is known from the southern continents. The peculiar plagiosaurs, presumably descended from brachyopids of the earlier Triassic, also make their sole appearance at this time in the form of four European genera — *Plagiosaurus, Plagiosuchus, Plagiosternum* and *Gerrothorax*; their presence in Asia and Australia is not established and they appear to be absent in North America. Three families — two trending to forms of very large size, the third extremely specialized — constitute, thus, the final labyrinthodont fauna. It is notable that all three trend toward the "stereospondylous" type of vertebral structure once believed characteristic of Triassic labyrinthodonts as a whole.

Australopelor was recently described, as a labyrinthodont, on the basis of a jaw fragment from the Jurassic(?) Marburg Formation of Queensland. If this should be confirmed, it would be the geologically latest occurrence of any labyrinthodont; but neither the nature of the specimen nor the age of the formation appear to be too well established.

Despite scepticism of this and other, earlier, reports of labyrinthodonts in the Jurassic, it is not impossible that some of these amphibians lingered on into that period. Absence of material is, as Nopcsa (1934, p. 84) has pointed out, no proof of the absence of these forms, for early Jurassic deposits are almost uniformly of the Liassic marine type, in which there are almost no remains of non-marine vertebrates of any sort.

In their earlier history the labyrinthodonts presumably gave rise to other amphibian groups and to the reptiles as well. Before the end of the Carboniferous, however, they had become a self-contained group, following, with considerable parallelism, a complicated evolutionary pattern. Even in the Triassic the labyrinthodonts were numerous and moderately varied. What caused their extinction at or near the close of that period cannot be determined in any simple fashion. Changes in food materials and climatic and physiographic changes may have been important, but are difficult to evaluate. Drought conditions postulated for the Keuper and its equivalents may have been influential. But certain forms were still present in the Rhaetic, when the oncoming of the Lias with its areas of shallow

seas suggests an amelioration of conditions in lowland areas. Advances among the fishes, with the replacement of palaeoniscoids by subholosteans and, in the Jurassic, by holosteans and early teleosts, may have affected piscivorous forms. A major factor, in all probability, was the development among the reptiles of a variety of water-dwelling types which effectively supplanted the now archaic labyrinthodonts.

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EXPLANATION OF ABBREVIATIONS

a, angular
ar, articular
art, articular socket in pterygoid (and epipterygoid) for basipterygoid process
art e, articulation for epipterygoid

bo, basioccipital
bpt, basipterygoid
bpt p, basipterygoid process
bs, basisphenoid

c, coronoid
cart ot, otic cartilage
cr, conical recess
crp, crista parotica

d, dentary

e, epipterygoid
ec, ectopterygoid
eo, exoccipital
et, tympanic excavation

f, frontal
fo, fenestra ovalis
fpt, posttemporal foramen

gr pal, groove for palatine artery
gr ic+pal, groove for internal carotid and palatine arteries

ic, internal carotid artery
ina, internasal
inf, interfrontal
in or, interorbital canal
it, intertemporal

j, jugal

l, lacrimal

m, maxilla

n, nasal

op, opisthotic

p, parietal
pa, prearticular
pal, palatine artery
pf, postfrontal
pl, palatine
pm, premaxilla
po, postorbital
pop, preopercular
pos, postsplenial
pp, postparietal
pr, prootic
prf, prefrontal
ps, parasphenoid
pt, pterygoid
ptf, posttemporal fossa

q, quadrate
qj, quadratojugal

sa, surangular
se, sphenethmoid
sm, septomaxilla
soc, supraoccipital
sp, splenial
sq, squamosal
st, supratemporal

t, tabular

v, vomer

II-XII, nerve foramina

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AT HARVARD COLLEGE
VOL. 99, NO. 2

STUDIES OF SOUTH AMERICAN PSAMMOCHARIDAE

PART II

BY NATHAN BANKS

WITH ONE PLATE

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
MAY, 1947

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OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT HARVARD COLLEGE

The Bulletin and Memoirs are devoted to the publication of investigations by the Staff of the Museum or of reports by specialists upon the Museum collections or explorations.

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No. 2—*Studies of South American Psammocharidae. Part II* [1]

By Nathan Banks

This paper concludes my studies of South American species in this family. The first three subfamilies were treated in Bull. M.C.Z., vol. 96, no. 4.

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Subfamily PSAMMOCHARINAE

This subfamily is readily separated by the absence of a groove on the second ventral segment, or any trace of it; by the absence of teeth on hind tibiae, and the presence on both mid and hind tibiae of moderately long, more or less irregularly placed spines; tip of the tibiae with a few spreading spines; usually with some small spine-pits on upper side of hind femora near tip; and by a depression, or pocket, in the base of the third discoidal cell.

Many species are wholly or almost wholly black, a few generally rufous or yellowish, and some have spots on the body or bands on the fore wings. Some species of Psammochares have spots of silvery or golden pubescence.

Most of the species have the antennae situate more or less above the upper margin of clypeus; several genera have them placed at the clypeal margin, and most of these have the front femora more or less thickened; these are the Pedinaspini; some species with but two submarginal cells, the Aporini. Bradley in a recent paper (1944) uses seven tribes. There are groups of genera, but many of the characters used are (to me) little more than generic characters, and sometimes not constant in specimens of one species.

Moreover, (to me) there are alliances between genera in different tribes, such as Sericopompilus and Euplaniceps, in the large stigma, the median row of spines on hind tibiae, etc.

[1]Published with the aid of a special gift from Mr. G. R. Agassiz.

For purposes of classifying them for determination I consider it much simpler to abandon these tribes entirely, and use whatever structures appear most definite and easily observed, irrespective of affinities.

Table of genera

Females

1. A comb to front tarsus 2
   No comb to front tarsus 14
2. No spines under last joint of hind (and usually mid) tarsus; tip of abdomen with only fine hairs 3
   At least a few spines under last joint of hind (and usually mid) tarsus 5
3. Tip of propodeum on each side extended backward into a process or large tooth; claws toothed; tip of abdomen with fine hairs; usually but two submarginal cells; small species; stigma minute ..... *Aporinellus*
   Tip of propodeum does not extend backward on each side 4
4. Claws toothed; no scales on basal segment nor propodeum; hind tibia with a median row of small spines between the two rows above; stigma slender, reaching far into the marginal cell ..... *Sericopompilus*
   Claws cleft; basal segment of abdomen and part of propodeum with appressed scales and also upright hair, fore wings fold lengthwise, thus a line of fold through the second discoidal cell ..... *Episyron*
5. Marginal cell almost twice its length from wing-tip, propodeum broad in middle and plainly, though not coarsely, striate; stigma longer than first abcissa of radius ..... *Aridestus*
   Propodeum not transversely striate; marginal cell usually nearer tip of wing 6
6. Antennae very short, third joint (and others) hardly twice as long as broad; tip of abdomen with fine hairs ..... *Sophropompilus*
   Joints of antennae longer 7
7. Stigma longer than first abcissa of radius, its tip oblique; body never wholly black; wings never wholly black; marginal cell long; clypeus large; claws often cleft 8
   Stigma rarely longer than first abcissa of radius, or if so wings or body black 9
8. Upper edge of clypeus deeply angularly emarginate each side, like a very low broad W; propodeum evenly rounded; front femora with small bristles near tip ..... *Batazonus*
   Upper margin of clypeus a nearly even curve, no spines nor

bristles on front femora above; propodeum often more or less humped each side behind, concave in middle....*Arachnophroctonus*

9. Claws cleft; tip of abdomen with fine hairs, no stout bristles..*Austrochares*
Claws toothed..... 10

10. Tip of abdomen above with only fine, more or less curved hairs 11
Tip of abdomen above with some stout, nearly straight bristles, usually in a group..... 12

11. Clypeus emarginate in middle of lower margin; body and legs very smooth; fore wings can fold lengthwise.....*Aplochares*
Clypeus never distinctly emarginate, although lower margin may be slightly, broadly concave.....*Pycnopompilus*

12. Clypeus with a distinct notch in middle of lower margin, not evenly concave across its width.....*Notiochares*
Clypeus without a median notch, but sometimes more or less broadly concave across its width..... 13

13. Propodeum without hairs above; marginal cell short, triangular, and much more than its length from tip of wings; third submarginal petiolate, or at least triangular.....*Pompilinus*
Propodeum rarely without hairs above; marginal cell longer; third submarginal not petiolate, rarely triangular; mostly larger species.....*Psammochares*

14. Stigma short, not or scarcely reaching into marginal cell; three submarginals; eyes not hairy; front femora little thickened; antennae not set in a large depression, nor close to clypeus..... 15
Pronotum often elongate; front tarsi short; stigma longer, often extended into marginal cell; front femora usually plainly thickened, antennae close to clypeus..... 17

15. Claws cleft; labrum well exposed, malar space sometimes quite long.....*Allocyphonyx*
Claws toothed; labrum not or scarcely exposed..... 16

16. Some spines under last joint of mid and hind tarsi; stiff bristles at tip of abdomen.....*Anoplius*
No spines beneath last joint of hind tarsi; fine hairs at tip of abdomen above.....*Neanoplius*

17. Only two submarginal cells; face with a depression each side; front femora strongly enlarged; anal in hind wings ending much before forking of cubitus..... 18
Three submarginal cells..... 20

18. The depression near each antennae extends upward, second recurrent ending second submarginal cell; abdomen elongate; eyes not hairy; basal vein ends at transverse.....*Euplaniceps*
The depression extends laterally from antennae; smaller species 19

19. Eyes plainly hairy ..... *Notoplaniceps*
Eyes bare ..... *Aporus*

20. Eyes not hairy; in hind wings anal vein ends at or close to forking of cubitus; second submarginal cell four-sided; clypeus flattened in middle; propodeum concave behind; tip of abdomen compressed ..... *Psorthaspis*
Eyes plainly hairy; in hind wings anal vein ends far before forking of cubitus, second submarginal cell rather five-sided; clypeus short and broad; tip of abdomen not compressed 21

21. Pronotum rather short, angularly emarginate in middle behind ..... *Epicostethus*
Pronotum much longer, not or scarcely emarginate behind ... *Aulocostethus*

The genus Lepidocnemis Haupt, based on one species *L. antiquus* Haupt from Argentine is unknown to me; perhaps it is African.

Batazonus Ashmead

This genus, the most primitive of the subfamily, contains many species in the Neotropic area, and some are common and widespread. The stigma is quite long, and the marginal cell also. The upper margin of clypeus is deeply indented each side. Most of them have the bodies partly pale or yellowish, and the wings usually hyaline.

Synopsis of females

1. Claws bifid on mid and hind legs as well as on front legs, at least the tooth is long and slopes toward tip 2
Claws of mid and hind legs with a short, erect median tooth .. 3

2. Fore wings yellowish with a brown tip and a dark spot in second submarginal cell; abdomen rufous, tips of several segments black ..... *rubricatus*
Fore wings mostly dark brown; abdomen mostly brown; several segments with a pale yellowish band across base ..... *exquisitus*

3. Marginal cell longer than space to wing-tip; third submarginal cell usually fully as long as second 4
Marginal cell shorter than space to wing-tip; third submarginal cell often shorter than second 7

4. Face yellowish, a large black spot above antennae, mesonotum black, with two yellow lines ..... *eurymelus*
Face dull yellowish to brownish or rufous; no distinct black spot above antennae 5

5. Mesonotum yellowish, with three brown streaks; abdomen with two pale bands, beyond deep black; fore wings yellowish ... *decedens*
Fore wings brownish; mesonotum a uniform rufous or darker .. 6

6. Femora rufous to brownish ..... *fervidus*
Femora and coxae deep black, rest of legs much paler ..... var. *intensivus*

7. Whole body pale yellowish to rufous, hardly a trace of the supra antennal mark, nor the dark on mesonotum, yellow band on abdomen scarcely paler than rest ..... *inornatus*
Black mark above antennae distinct or whole face black; also the mesonotum black or largely so 8

8. Face almost entirely black, also clypeus; sometimes the orbits pale; costal half of fore wings very dark 9
Face and clypeus with much more yellowish 10

9. Head, thorax, and abdomen usually almost wholly black, legs also the clypeus ..... *costatus*
Head and apical part of abdomen mostly black, thorax and legs mostly red-brown to yellow-brown or paler; clypeus yellow on lower half ..... *oenochrous*

10. Pleura nearly uniform yellowish to pale yellowish brown, no distinct black spots; pronotum the same, hind femora usually wholly pale 11
Pleura and pronotum pale, plainly marked with black; hind femora often partly black 12

11. Abdomen pale brownish, with yellow band across base of first, second, and often third segment ..... *polistoides*
Abdomen pale on first and most of second segments, rest black or nearly so ..... *apicalis*

12. All femora pale; median dark stripe on propodeum not quite reaching posterior dark mark; third antennal joint scarcely if any longer than vertex-width ..... *familiaris*
Femora, at least hind ones, marked with black, sometimes also on hind tibiae; mid stripe of propodeum complete, reaching apical border 13

13. Last two or three segments of abdomen wholly pale, others with broad basal pale band; venter almost wholly pale ..... *flavopictus*
Last two or three segments of abdomen almost wholly black, venter largely black ..... *ventralis*

Males

1. Scutellum pale, dark each side, propodeum with broad pale band across tip, fore wings with tip dark; marginal cell as long as space to tip of wings, but end of third submarginal cell nearer to second cell than to outer border of wing 2
Scutellum dark, usually pale spot each side 3

2. Face and clypeus wholly black, a small, short species ..... *autrani*
Face and clypeus with broad pale stripe each side up to vertex; a small, rather stubby species ..... *exiguus*

3. Marginal cell plainly longer than space to wing-tip; end of third submarginal cell nearer to wing border than to end of second submarginal cell 4
   Marginal cell not longer than space to wing-tip; end of third cell nearer to end of second than to outer border 5
4. Abdomen rufous, some segments with narrow black apical margin; fore wings yellowish to rufous ..... *fervidus*
   Abdomen black above, pale band at base of first, second, and third segment; fore wings yellowish brown ..... *eurymelus*
5. Face and clypeus almost wholly black, orbits usually narrowly pale; costal part of wings dark 6
   Clypeus at least, and usually face with more pale 7
6. Thorax black, femora usually partly black ..... *costatus*
   Thorax with much rufous, femora rufous; lower half of clypeus rufous ..... *oenochrous*
7. Pleura wholly pale 8
   Pleura with distinct black marks 10
8. No black on mesonotum above, at most yellowish brown; propodeum unmarked, very pale throughout; abdomen with first three segments wholly pale ..... *inornatus*
   Some black on mesonotum; first, second, and third segments of abdomen dark, with basal pale band 9
9. Hind tarsi wholly dark brown to black; apical half of abdomen above and below black ..... *apicalis*
   Hind tarsi mostly pale; abdomen dull reddish brown, first, second, and third segments with basal yellow band ..... *polistoides*
10. Median black stripe on propodeum reaches to tip; fore wings with costal half a nearly uniform yellowish ..... *flavopictus*
    Median black stripe usually hardly halfway to tip; first submarginal cell clear hyaline, blackish beyond ..... *familiaris*

Batazonus fervidus Sm. (Pompilus)

From Kartabo, 24 March, 30 June; Bartica, 4 Febr., both British Guiana; Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert); Villa Rica, Paraguay, Dec. (F. Schade); Alausi, Ecuador, 19 June; Mendoza, Argentina, 6 December, (Joergensen); Nova Teutonia, Santa Catharina, 6 January (Plaumann); Chapada, Santarem, Rio de Janeiro (H. H. Smith).

Batazonus fervidus var. intensivus var. nov.

Differs from typical form in having coxae black, also femora, and large black marks on pleura. Thorax, propodeum much darker than

normal, both wings more nearly black. The comb-spines are plainly shorter, those on basitarsus hardly one-half of basitarsus, the apical one not equal to second joint of tarsus.

From Mayaro Bay, Trinidad, 25 Sept. (N. A. Weber). Type M. C. Z. no. 26599.

Batazonus ventralis spec. nov.

Female. Head pale yellowish, the horseshoe black mark above antennae is connected over vertex to ocular line and back to the black on occiput, a nearly square dark spot in middle of clypeus; antennae yellowish on basal joint, second and third black, fourth and fifth yellowish, rest black. Pronotum pale, with a large broad, brownish band across front and extending back on sides; mesonotum black, with the two yellow stripes very narrow and rather widely divergent in front; scutellum black, with an elliptical yellow spot each side; propodeum dull yellowish, with a median black stripe and one each side; black mark on mesopleura, and another on metapleura, also on mid and hind coxae.

Abdomen almost wholly deep black, base of first segment with two yellow spots, a yellow band across base of second segment, base of third rather pale; venter almost wholly dark except the base. Legs pale yellowish, mid and hind femora streaked with black, and sometimes hind tibia darkened. Fore wings with costal half mostly yellowish brown, but beyond the cells without the yellowish.

Third joint of antennae about as long as vertex-width; comb-spines rather short as in *flavopictus*; inner spur of hind tibia reaching plainly beyond middle of basitarsus; in fore wing marginal cell not quite so long or so sharply pointed as in *flavopictus*; second recurrent curved and ends plainly beyond middle of third cell, latter with outer side about as long as the lower side.

Length of fore wing 12 mm.

From Nova Teutonia, Santa Catharina, Brazil, 4 January, (F. Plaumann). Type M. C. Z. no. 26602.

Batazonus polistoides Sm. (Pompilus)

From Kartabo, 13, 29 May; Rio Mazaruni, Forest Settlement, Aug.-Sept. (Weber); Demerara Riv., 18 Febr., 8, 19 March; Bartica, 16, 27 Jan., 12 Febr., all in British Guiana. Restrepo, Dept. Meta, 500 M.; Muzo, Dept. Boyaca, 900 m., both Colombia, taken by Bequaert; Rio de Janeiro, Brazil (Lane); Villa Rica, Paraguay (Schade);

Province Sara, Bolivia (Steinbach). Chapada, Corumbá, Marurio, Santarem, Rio de Janeiro (H. H. Smith); and Waranama, British Guiana, 15 Nov. (Ogilvie), Amer. Mus. Nat. Hist.; Mt. Duida, Venezuela, 4 November (A. M. N. H.).

Batazonus eurymelus spec. nov.

Male. Face and clypeus yellowish, above antennae is a large, nearly triangular black mark enclosing a yellow spot, antennae yellowish brown, darkest toward tip; pronotum dull yellowish, with a dark patch each side in front; mesonotum black, with two yellow stripes somewhat diverging in front, and a narrow yellowish streak just within the tegulae, scutellum black, a yellow spot each side; propodeum dull yellowish with a brownish patch each side; pleura yellowish gray; abdomen above black, first segment with broad basal yellow band, but extreme base black, a yellow band at base of second and third segments, other segments faintly pale at base, not yellowish, rather greenish; venter pale on basal half, beyond partly dull black; legs pale yellowish, some tarsal joints darker at tip, hind tarsi and tibiae almost black, and hind femora dark near tip; fore wings with costal half pale yellowish brown.

The antennae are thick and crenulate, but the joints are not so long, particularly on basal half of flagellum as in *fervidus*; on hind tibiae the inner spur fully two-thirds of basitarsus; in fore wing the marginal cell is much longer than space to wing-tip, the third submarginal cell longer below than second, narrowed to nearly one-third above, second recurrent vein ends at middle.

Length of fore wing 11.5 mm.

From Nova Teutonia, St. Catharina, Brazil, 11 Jan. (F. Plaumann). Type M. C. Z. no. 26600.

It is peculiar in that it has the markings of species of the section with the short marginal cell.

Batazonus flavopictus Sm. (Pompilus)

Described from Central America, where it is not uncommon. Northern South America; Vista Nieve, Santa Marta 5,000 ft., 12 January, 9 February (G. Salt); Vista Nieve, San Lorenzo Mt., 19, 21 December (Bequaert); Muzo, Dept. Boyaca, 900 m. (Bequaert), all Colombia, and one from Paramaribo, Surinam; between Queremal and Buenaventura, Colombia, 3,500 to 4,000 ft., 12 February (A. M. N. H.).

Batazonus apicalis spec. nov.

Female. Head yellowish, with the usual black horseshoe mark above antennae, occiput mostly pale, darker around aperture, basal joint of antennae yellowish, rest rufous and dark or black on apical part, and often on some joints near base, at least above, sometimes wholly black. Pronotum dull yellowish, mesonotum black or dark brown with the usual two yellow stripes; scutellum reddish brown in middle, yellowish on sides; propodeum yellowish, usually unmarked but sometimes a narrow median rufous stripe; pleura yellowish, no black; legs pale yellowish, tips of hind tarsal joints dark.

Abdomen pale on first and usually also on second segment, or part thereof above and below, rest of abdomen black, but sometimes third segment has a basal pale band. Fore wings with costal half yellowish brown, often darker than in *polistoides*. Structure similar to *polistoides*, third antennal joint a little longer and fourth a little shorter, and other joints shorter; inner spur of hind tibia full half of basitarsus, tibia above with spines hardly as long as in *polistoides*; in fore wings the marginal cell is shorter than space to wing-tip, second recurrent ends plainly beyond middle of third submarginal cell, latter with outer side nearly as long or longer than lower side.

Length of fore wing 11 to 14 mm.

From Hohenow, Alta Parana; Cerro Pelado, and Villa Rica, all in Paraguay, in December, January, and February (Schade). Also one from Col Perene, Peru, 25 June (Cornell Univ. Exped.). Type M. C. Z. no. 26601; paratypes there and at Cornell Univ.

Batazonus familiaris Sm. (Pompilus)

From Chapada, Brazil (H. H. Smith); Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert); Villa Rica, Paraguay, February (F. Schade); and Kartabo, British Guiana, 15 December. Corumba and Uacarizal, Brazil (H. H. Smith).

Batazonus costatus Taschenb. (Pompilus)

From Santa Cruz, Bolivia (Steinbach); Villa Rica, Paraguay, 9 May, 1 March (F. Schade); Nova Teutonia, Santa Catharina, Brazil, 24 November, 25 December (Plaumann). Chapada, Corumba, Santarem, Brazil (H. H. Smith); Campinas, Brazil, February (Williams), and Jabaty, Para, Brazil, May (Williams).

Typical *costatus* is almost wholly black, clypeus wholly black; variations show yellowish stripes on thorax and marks on base of abdomen.

Typical *Pompilus vinicolor* Fox has a black head, and a stripe on each side of mesonotum; specimens from Villarica and Campinas have clypeus rufous on lower part, some have rufous thorax more or less striped; these show a tendency of *vinicolor* Fox to grade into *costatus* Taschb.; at most I think *vinicolor* can be only a variety or color phase of *costatus*. Since *vinicolor* Fox is preoccupied by *Pompilus vinicolor* Packard (a Cryptochilinid) Schulz proposed *oenochrous* for the Fox *vinicolor*; thus

Batazonus costatus var. oenochrous Schulz

Specimens from Chapada, Brazil (paratype of *vinicolor* Fox); Villarica, Paraguay (Schade coll.).

Batazonus exiguus spec. nov.

Male. Body black, marked with yellowish; face and clypeus with a broad yellow stripe each side, narrowing to a point at vertex, no median yellow stripe above antennae, latter yellowish on basal joint below, darker above, rest rufous, tips of joints very narrowly black; pronotum with broad yellow band behind, scutellum and postscutellum both entirely yellowish; propodeum with a broad, almost white band over most of apical half; no pale on pleura; first segment of abdomen with pale yellow band before middle, extreme base black, segments two to five with yellowish basal bands (sometimes obscured in retraction); venter black from beyond middle of second segment; tips of front coxae nearly white; front and mid femora pale at tips; all tibiae mostly pale above; all tarsi pale, nearly white, tips of joints black; wings nearly hyaline, a brown cloud beyond third submarginal cell to wing-tip; stigma almost wholly dark brown, darker than in other species.

In structure much like male of *B. familiaris*; the propodeum more flattened, and mesonotum less arched, legs hardly as slender. In fore wings marginal cell is about its length from wing-tip, second submarginal only a little longer than broad, scarcely narrowed above, receiving the first recurrent vein at middle; third submarginal cell about as long below as second, less than half as long above, outer side nearly straight, receiving the second recurrent beyond middle.

Length of fore wings 5.5 mm.

One male from Vista Alegre, Rio Brancho, Amazonas, Brazil (Bequaert). Type M. C. Z. no. 26781.

Batazonus inornatus Banks

Described from several specimens from Rio Frio, Magdalena, Colombia, July (Salt).

Batazonus exquisitus Fox (Pompilus)

One from Annapolis, Goiaz, Brazil (Fairchild). Described from Chapada, Brazil.

Batazonus rubricatus Sm. (Pompilus)

One from Negritos, Peru, July (Mrs. Frizell). Only species seen from west of the Andes.

Batazonus decedens Sm. (Pompilus)

From Kartabo, British Guiana, 26 February, 4 March, 3 June; Iquitos San Rogue, Peru, March (Klug coll.) Cornell Univ. collection; Santarem, Brazil (H. H. Smith); Tukeit, British Guiana, 16 August, and Iquitos, Peru (Amer. Mus. Nat. Hist.).

Batazonus autrani Holmb. (Pompilus)

One from Mendoza, Argentine, 12 December (Joergensen). *Agenia multipicta* Smith, and *A. decepta* Smith are possibly males of Batazonus; *Pompilus falvus* Fabricius may belong to this genus.

Arachnophroctonus Ashmead

The species are related to Batazonus in many ways, but the propodeum is concave in middle of posterior slope and the sides often swollen, angularly protuberant, or even tuberculate. The front femora have no spine at upper tip, and tibiae less spinose than Batazonus; none of the species are black, but more or less rufous to yellowish; there are no small fine bristles on the front femora.

All the species (except *xanthopterus*) were described in Pompilus, but Dalla Torre places several of them in Salius.

Females

1. Wings very dark, especially on costal half; abdomen dull reddish brown; propodeum with a distinct tubercle each side at about middle of length ..... *vulpes*
   Wings hyaline, or yellowish, frequently one or two dark spots or bands in front pair 2

2. Abdomen without a dark band, body about ten to twelve millimeters; wings unmarked ..... *rubiginosus*
   Abdomen with at least one dark, often black band 3

3. Propodeum with a distinct raised tubercle on each side, not simply angulate 4
   Propodeum at most angularly swollen each side, not elevated into a cone or tubercle 5

4. Fore wing plainly rather bright yellowish, not marked with brown, veins yellowish ..... *xanthopterus*
   Fore wings not so plainly yellowish; the basal vein slightly bordered with brown, a brown band or spot behind marginal cell, and upper tip darkened ..... *mendozae*

5. Propodeum not the least angulate on sides; third antennal joint much longer than vertex-width; hair on front, front coxae, and propodeum behind longer than usual, marks on abdomen hardly complete ..... *pallidus*
   Propodeum angled on sides; hair shorter 6

6. Fore wings without dark band over basal vein and behind marginal cell, rather evenly yellowish except tip 7
   Fore wings with basal vein bordered or spot behind marginal cell, usually both 8

7. Third antennal joint much longer than vertex-width; propodeum only slightly angled or swollen on sides; large species, 16 to 20 mm ..... *erubescens*
   Third antennal joint but little longer than the vertex-width; propodeum plainly but not strongly angled on side; small species 10 to 12 mm ..... *rubiginosus*?

8. Coxae and pleura deep black; a black line from eye to eye through ocellar area ..... *latus*
   Coxae and pleura largely yellowish or rufous; line from eye to eye 9

9. Pronotum almost wholly the vertical front; propodeum not elevated in middle part of base ..... *torridus*?
   Pronotum curved and sloping in front; middle part of base of propodeum elevated ..... *affinis*

Males

1. Subgenital plate not carinate along middle, but transversely rounded ..... *erubescens*
   Subgenital plate carinate along middle 2
2. No dark marks or bands in fore wings 3
   Dark mark behind marginal cell, and often over basal vein 4
3. Ocelli situate on a black spot; venation very dark ..... *virulentus*
   Ocelli not on a black spot; venation pale ..... *xanthopterus*
4. Propodeum angulate on sides ..... *mendozae*
   Propodeum not angled on sides ..... *rubiginosus*

ARACHNOPHROCTONUS MENDOZAE Dalla Torre (SALIUS)

Described from Mendoza, Argentine; I have seen several specimens of both sexes from that locality taken by C. E. Reed (Cornell) and Joergensen, latter in December; other Argentine localities are La Rioja (Giacommelli); San Juan, 18 December; Cosquin, Sierra de Cordoba, 1 to 9 March (Cornell).

Described as *Pompilus tuberculatus* Smith, 1879, it was preoccupied by Smith himself. *Pompilus rutilans* of Fox, from Brazil appears to be the same species; it was published in November 1897, *mendozae* in May 1897.

ARACHNOPHROCTONUS XANTHOPTERUS Rohwer

Females from Sapucay, and Villa Rica, Paraguay (Schade). A male from Malinescue, Paraguay (Schade). The wings are a brighter yellow than in most other species; the tubercle on each side of propodeum is blunt.

ARACHNOPHROCTONUS ERUBESCENS Taschb. (POMPILUS)

This very large species was described from Banda Oriental, Parana; Mendoza; and Rio Janeiro. Several specimens from Mendoza, La Rioja, Argentine; and from Uruguay, are before me. The subgenital plate of the male is not carinate in middle.

Quite probably this should be credited to Spinola and date from 1841 (French Annales) since in describing *bituberculatus*, he gives enough notes of comparison based on the specimen Klug loaned him to hold the name.

ARACHNOPHROCTONUS VULPES Dalla Torre (POMPILUS)

Specimens from Kartabo, British Guiana, 11 June; and Santa Cruz, Bolivia (Steinbach); Blairmont, British Guiana, September (Williams). It was described by Spinola as *Pompilus bituberculatus* from Cayenne, a name which was already used by Guerin, and the *Pompilus crassidentatus* Cameron from Demerara appears to be the same.

ARACHNOPHROCTONUS AFFINIS spec. nov.

In coloration like *mendozae*, but more than outer half of antennae black, as in *vulpes*; the brown marks in fore wing are scarcely as distinct as in *mendozae*, and general surface of wing more hyaline, less yellowish. The propodeum has the posterior sides only slightly swollen, not even as much as in *latus*, but more than in *pallidus*. From side view the middle part of the base of propodeum is much elevated above the hump of spiracles, similar to *mendozae* and *xanthopterus*, more than in other species (in *pallidus* not at all elevated above the hump of spiracles. The head and propodeum is quite hairy, but that on head and front coxae, and propodeum not so long as in *pallidus*. Venation similar to *mendozae*, but the second recurrent vein rather more sinous; face and ocelli about as *mendozae*.

Length of fore wings 15 mm.

Type from Maracajú, Matto Grosso, Brazil, April-May (Fairchild), also Villa Rica, Paraguay (Schade); both females.

Type M. C. Z. no. 26705.

ARACHNOPHROCTONUS LATUS Smith

From Cosquin, Sierra de Cordoba, Argentina, 1 to 9 March (Cornell Univ. Expedition); Piracicaba, Brazil, February (Williams). Several specimens. Readily known by the black pleura and mid and hind coxae; the black at base of mesonotum is much broader than in other species. The propodeum is angularly protuberant each side where the tubercle is in *tuberculatus*. Venation much as in that species except that the second recurrent vein is angularly bent instead of the curve of the related species.

ARACHNOPHROCTONUS VIRULENTUS Smith (POMPILUS)

A male from Muzo, Dept. Boyaca, Colombia, 900 m., June (Bequaert) agrees with this Central American species; the veins and

stigma much darker than in other South American species, except *vulpes*.

ARACHNOPHROCTONUS PALLIDUS spec. nov.

Body pale yellowish rufous, sutures on thorax above only very narrowly black, pleura with scarcely any black, propodeum behind with a small quadrangular, median black spot; abdomen with a dark band at tip of first and of second segments, distinct only laterally, broken in middle, ventrally second segment dark behind; mid and hind legs with tips of tarsal joints faintly dark. Wings yellowish, fore wings with basal vein dark and faintly bordered, a dark spot at end of second submarginal cell, spreading a little into discoidal cell, costal tip darkened.

Clypeus and face much as in *mendozae*, but vertex and ocellar triangle a little more narrow. Structure in general much like *mendozae*, except the propodeum, this is more slender, and not even angularly broadened, not protuberant, the spiracles are also less prominent. The hair on front and propodeum, especially behind is longer and more dense; there is no difference in venation from *mendozae*.

Length of fore wings 13 mm.

One female from Matucana, Peru, 1 May (Cornell Univ. Expedition).

ARACHNOPHROCTONUS RUBIGINOSUS Taschb. (POMPILUS)

The original description is very short, and mostly comparison with *erubescens*; the size was 11 mm. It was said to have no dark bands on abdomen; I have not seen any species which did not have at least one dark band. However, a small female from Cordova, Argentine (Davis) has the wings evenly yellowish, except the tips, the propodeum is slightly angled each side, but otherwise much like *erubescens*; from side the middle part of base of propodeum is not elevated above spiracles. It may not be *rubiginosus*. A male from Buenavista, near Santa Cruz, Bolivia (Cornell coll.) is about same size; the propodeum not angled, much as in male of *erubescens*, the wings are nearly hyaline; the subgenital plate is carinate in the middle, this may not be the male of the Cordoba female, nor the true *rubiginosus*, since the black band at tip of first segment is distinct.

ARACHNOPHROCTONUS sp. TORRIDUS Cress.?

A specimen, labelled "Trinidad" is probably related to *A. torridus* Cresson from Mexico, but it differs in some minor points.

Psammochares Latreille

The female has a definite comb, the last joint of mid and hind tarsi has some median spines, the claws are toothed, tip of abdomen with some very stiff stout bristles, propodeum usually hairy above, the marginal cell is moderately long. A few species here included have no hair on propodeum, but the marginal cell is fairly long and the third submarginal cell not pedicellate nor triangular, so cannot go in Pompilinus; the latter genus needs a new definition.

I have left in this genus several species that may not belong here; the males of *separatus*, *inaurata*, and *inculcatrix* have a velvety pad on fourth ventral segment, and the subgenital plate is forked just as in males of Notiochares.

Females

1. Pronotum bordered behind with silvery or pale yellowish.... 2
   Pronotum wholly black.... 11

2. Abdomen entirely black; thorax with spots of silvery or golden pubescence.... 3
   Abdomen at least partly rufous.... 5

3. The propodeum has a white spot each side near hind margin, not extending forward; hind border of pronotum with silvery pubescence.... *argenteomaculata*
   The white or yellowish pubescence near hind border of propodeum extends forward.... 4

4. The yellowish spots reaching forward almost to base of propodeum, leaving a median black streak.... *inaurata*
   The silvery spots reaching forward in a curve to meet in middle thus enclosing an elliptic dark area; face silvery.... *marginicollis*

5. Abdomen wholly rufous above.... 6
   Abdomen with some segments more or less plainly bordered behind with dark.... 8

6. No silvery mark on mesopleura, or extremely faint; hind legs wholly black.... *torquata*
   A prominent silvery spot on lower mesopleura, hind legs beyond femora plainly rufous.... 7

7. Wings brown; third antennal joint nearly twice the length of the first joint.... *personata*
   Wings nearly black; third antennal joint not nearly twice the length of the first joint.... *turcica*

8. No distinct silvery mark on mesopleura; no hairs or only faint ones on propodeum ..... *argelesia*
   A distinct silvery spot on mesopleura 9

9. Only three segments with rufous above, the third divided; spots on thorax golden to yellowish ..... *pulchrisoma*
   Some rufous on fourth segment; spots silvery 10

10. Spots on propodeum confined to tip ..... *inculcatrix*
    Spots on propodeum reach forward ..... *triquetris*

11. Abdomen with a white or creamy spot on each side (not above) of second segment ..... *veranes*
    No such spots, but sometimes rufous above on some segments 12

12. Abdomen at least partly rufous 13
    Abdomen without rufous, wholly dark 24

13. Abdomen wholly rufous, fourth abcissa of radius about one-half of costal length of marginal cell; third cell very narrow above ..... *boliviana*
    Abdomen dark, at least on some apical segments 14

14. Abdomen rufous on but one segment, the second 15
    Abdomen rufous on more than one segment 16

15. Comb-spines very long, usually four, but basal often shorter; hair on face very short; no blue on body ..... *platensis*
    Comb-spines of moderate length, but three on basitarsus; hair on face very long and dense; body more or less bluish ..... *semicincta*

16. Basal segment wholly black, second and third segments largely rufous above; third cell narrow above; fourth abscissa of radius about one-half costal length of marginal cell ..... *peruviana*
    Basal segment at least partly rufous 17

17. Third segment wholly black 18
    Third segment rufous at least on basal part 19

18. First segment bordered behind with black, second segment almost divided by black; first segment black on venter ..... *arequipensis*
    First segment not plainly bordered, second not divided, first segment on venter partly rufous ..... *bilunata*

19. Four segments rufous, each more or less plainly divided by dark so as to make eight rufous spots above; fourth abscissa of radius fully one-half costal length of marginal cell ..... *scalaris*
    Not showing eight spots above 20

20. Four long curved comb-spines on basitarsus ..... *hermanni*
    But three comb-spines on basitarsus 21

21. Comb-spines much longer than width of joint, second on basitarsus about reaching the one at tip 22
Comb-spines shorter, second on basitarsus not nearly reaching the one at tip, hardly more than one-half way; fourth abcissa of marginal cell not nearly one-half of costal margin of marginal cell 23

22. Vertex minutely striate; lateral ocelli plainly nearer each other than to eyes; in hind wings anal ends beyond forking of cubitus ..... *partita*
Vertex not striate; lateral ocelli about as near eyes as to each other; in hind wings anal ends little if any beyond forking of cubitus ..... *decepta*

23. First and second segments not bordered with dark behind; end of third submarginal straight, oblique; a large hyaline spot over second recurrent vein often spreading toward costal margin ..... *holmbergi*
First and second segments more or less plainly bordered with dark behind; fore wings nearly evenly dark; end of third submarginal cell curved and making the cell nearly triangular; little if any hair on propodeum ..... *separata*

24. Basal joint of antennae with long hairs; clypeus hairy all over, long hairs on head and propodeum; three comb-spines on basitarsus ..... *cymocles*
Basal joint of antennae scarcely if at all hairy 25

25. Four comb-spines on basitarsus 26
But three comb-spines on basitarsus 27

26. Body blue; comb-spines long, propodeum and front densely hairy ..... *atrimene*
Body black; comb-spines as long but thicker; propodeum and front only moderately hairy ..... *euacantha*

27. Clypeus plainly and broadly concave below 28
Clypeus barely if at all concave below 31

28. Propodeum wholly silvery above, two silvery bands on abdomen ..... *caloderes*
Propodeum at most with small silvery spots behind; no bands on abdomen 29

29. Outer side of third submarginal nearly straight and oblique .. 30
Outer side of third submarginal much curved, cell nearly triangular, last two or three segments ash-grey ..... *emortua*

30. First recurrent vein ends about one-third before end of second submarginal cell; pale in third discoidal cell, some silvery on collar, sides of metanotum, and on tip of propodeum ..... *alcataria*

First recurrent vein ends close to tip of second sub-marginal cell, third discoidal scarcely paler; collar only slightly silvery, no distinct silvery on sides of metanotum nor on tip of propodeum ..... *echinatus*

31. Abdomen deep blue; hind wings largely hyaline; third submarginal cell longer than second; face and pronotum densely hairy ..... *allorices*
Abdomen scarcely if at all bluish; hind wings dark; face and pronotum but little hairy 32

32. Third submarginal cell subtriangular, shorter than second; second plus third antennal joints not nearly equal vertex width ..... *cynthia*
Third submarginal cell much longer than second; second plus third antennal joints nearly equal vertex width ..... *vestoris*

The males of Notichares have a velvety patch on tip of fourth ventral joint; those of Anoplius have a brush of erect hair on fourth or fifth ventral segment; the antennal joints of Sophropompilus are very short.

The males of Psammochares and allied forms known to me are tabulated below. The names I have applied are somewhat tentative since it is not possible to associate the male with its true mate in many cases. Therefore I have included the males of some genera allied to Psammochares

1. Abdomen more or less reddish above 2
Abdomen without reddish above 12

2. Hind border of pronotum not pale, no spots on pleura, legs black; wings black 3
Hind border of pronotum pale 6

3. Abdomen wholly reddish above and below ..... *Austrochares satanus*
At least two or three apical segments black 4

4. Second and third segments of abdomen rufous above and on venter ..... *hermanni*
Venter wholly black; second segment with a large rufous or yellowish spot each side, nearly or quite touching 5

5. Basal joint of antennae hairy; head very densely long-haired, basal segment of abdomen hairy; spots occupying about one-half the length of segment ..... *semicincta*
Basal joint of antennae and basal segment of abdomen not hairy; head and pronotum less hairy; spots transverse, not occupying half the length of segment, often a pale dot each side on first segment ..... *bilunata*

6. Hind tibiae black or almost so 7
Hind tibiae yellowish to rufous; venter largely rufous 11

7. Abdomen almost wholly rufous above and below; pleura wholly black; fore wings hyaline in middle ..... *torquata*
Abdomen more or less black on venter 8

8. Venter wholly black, abdomen above with four or five segments rufous in front and bordered behind with dark or black, the rufous often interrupted in middle with dark; pleura black .... *scalaris*
Venter partly rufous 9

9. Fore wings evenly dark, nearly black 10
Fore wings hyaline between basal vein and the third submarginal cell; propodeum very narrowly white at each hind corner ..... *turcica*

10. Propodeum with only a little pale each side behind; fourth ventral segment with a velvety patch ..... *inculcatrix*
Propodeum with a large yellowish to pale spot each side behind, reaching nearly half-way to front ..... *triquetra*

11. Face snow-white; marginal and third submarginal cells hyaline; head only slightly hairy, basal vein not bordered with dark ..... *personata*
Face yellowish; marginal and third submarginal cells at least partly dark; head densely hairy; basal vein more or less bordered with dark ..... *taschenbergi*

12. Abdomen with some whitish, cinereous or ashy bands above on some segments before the sixth 13
Abdomen wholly black or bluish above, or slightly paler on last segment 19

13. Mesopleura with a large yellowish spot, also each side near end of propodeum; second, third and fourth segments with cinereous bands; wings and legs black; fourth ventral segment with velvety patch ..... *inaurata*
No yellowish or whitish on pleura 14

14. Abdomen with cinereous on only fifth, sixth, and seventh segments, venter wholly black; head and basal joint of antennae densely hairy; wings black ..... *emortua*
Venter with whitish or cinereous on first three segments, above with cinereous on some before the fifth 15

15. Whitish on base of first segment above and on tip of propodeum; wings evenly black ..... *caloderes*
Cinereous on at least third and fifth segments 16

16. No cinereous on fourth segment; wings mostly hyaline, dark only at tip ..... sp. x
Cinereous on fourth segment 17

17. Wings hyaline, the tip dark; propodeum silvery towards tip.....sp. y
Wings at least partly dark before middle, propodeum largely silvery..... 18

18. Wings wholly black or almost so.....*echinata*
Wings partly pale before stigma.....*ornamenta*

19. Basal joint of antennae very hairy in front; head pronotum, pleura also densely hairy.....*cymocles*
Basal joint of antennae not hairy..... 20

20. Antennae beyond middle undulate, narrowed at base, and bent down in middle below, concave above; pleura and pronotum but little hairy; outer side of third submarginal cell curved.....*Austrochares cordovensis*
Antennae not undulate; outer side of third submarginal cell nearly straight..... 21

21. Wings nearly evenly black; third submarginal cell almost higher than long; body mostly black.....*Austrochares elsinore*
Wings smoky, in places nearly hyaline; third submarginal much longer than broad; body strongly blue....*Neanoplius coeruleosomus*

Psammochares cynthia spec. nov.

Female. Black, dorsum of abdomen with slight bluish or greenish iridescence; wings nearly black on basal part, more brown toward tip, veins black, tibial spurs yellowish brown. Clypeus nearly three times as broad as long, truncate below; face very broad, little narrowed above; antennae short, slender, third joint scarcely more than two-thirds of vertex-width; hind ocelli much nearer each other than to eyes; very little and very short hair on head; pronotum angulate behind, with few and very short hairs; pleura scarcely at all hairy; propodeum short, evenly rounded, with much long hair above, basal part of first abdominal segment hairy above, last segment above with very few but plainly stout hairs or bristles, this segment somewhat compressed and much pointed, with few hairs below, but some short ones on sides, as also on sides of preceding segment.

Legs moderately short; comb of short but thick spines, four on basitarsus, the first short, the last about one-half of second joint; hind tibia with few and short spines, inner spur not one-half of basitarsus; claws toothed.

Fore wings with marginal cell fully its length before wing-tip, at top of third submarginal it is fully as broad as submarginal cell; second submarginal cell about as broad as long, base curved, receiving

the first recurrent vein at tip; third submarginal shorter than second, much narrowed above, outer side curved, receiving the second recurrent (slightly curved) at middle; extension of medius equal to length of third cell; basal vein interstitial with transverse; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 10 mm.

From San Ignacio, Argentine, 15 March (Joergensen). Type M. C. Z. no. 26231.

PSAMMOCHARES EMORTUA spec. nov.

Female. Black, abdomen above with very faint greenish iridescence, last two segments ashy-gray, wings nearly evenly dark brown, veins black, spurs brownish, face each side of antennae somewhat silvery. Clypeus about three times as broad as long, truncate below; face broad, a little narrowed above, vertex-width very much longer than the third joint of antenna, front with very short hair, ocelli in low triangle, laterals much nearer each other than to eyes; pronotum angulate behind, no distinct hair, nor on pleura; propodeum short and broad, from side evenly curved, with scant but moderately long hair above; no hair on first segment of abdomen above; this segment large and high, last segment somewhat compressed, above with fine gray pubescence and some stiff bristles, a number of long hairs on sides and below, a few on other ventral segments; legs rather stout and short, three slender comb-spines on basitarsus; last about one-half of second joint; hind tibiae with many short but stout spines above, inner spur hardly one-half of basitarsus, on mid tibia it is more than one-half of basitarsus; claws toothed.

In fore wings the marginal cell is not quite its length from wing-tip, at top of third submarginal cell it is broader than submarginal; second submarginal cell longer than broad, base oblique, receiving the first recurrent vein at tip; third submarginal shorter, much narrowed above, the outer side being curved, receiving the second recurrent (nearly straight) at middle, extension of medius much shorter than cell; basal vein interstitial with transverse; in hind wing anal vein ends at forking of cubitus.

Length of fore wing 13 mm.

From Cordova, Argentine (Davis). Type M. C. Z. no. 26230. Paratype from La Rioja, Argentine (Giacomelli) (Cornell Univ. coll.). Two males from Santa Cruz, Bolivia (Steinbach) probably belong to this species since the last three segments of abdomen are ashy-gray

like the female, otherwise black; body much more slender, abdomen with nearly parallel sides; the head is densely long-haired, much longer than in the female; the venation about the same but one specimen has the third submarginal cell triangular; the clypeus and lower face are plainly silvery; also a male from Cosquin, Sierra de Cordoba, Argentina, 1 to 9 March (Cornell Univ. Exped.).

Psammochares euacantha spec. nov.

Female. Black; wings smoky brown, veins nearly black. Clypeus about two and one-half times as long as broad, lower margin straight in middle, a few hairs below middle; face scarcely narrowed above, vertex-width plainly longer than third antennal joint; ocelli in a low triangle, hind ones plainly nearer to each other than to eyes; hair on front short, mostly near eyes, vertex with longer hair; propodeum short, posterior slope steep, moderately densely haired above; mesopleura with some hairs.

Abdomen slightly depressed, tip with a few stout bristles, last ventral segment quite hairy under and on sides. Legs rather short, comb-spines moderately long; four on basitarsus, overlapping and thickened, last one reaching to tip of second joint; mid and hind tibiae with moderately long spines, inner spur of hind tibiae faintly curved and reaching a little beyond middle of basitarsus, on mid tibiae inner spur also slightly curved and reaching fully to middle of basitarsus; claws toothed.

In fore wings the marginal cell is more than its length from wing-tip, much broader than second submarginal cell, latter longer than broad, both ends oblique, receiving the first recurrent near tip, third submarginal cell much shorter below, end curves to top almost to a point, receiving the second recurrent (almost straight) a trifle before middle, extension of medius much longer than third cell; basal vein interstitial with transverse; in hind wing the anal vein ends scarcely before forking of cubitus.

Length of fore wing 8 mm.

From Buena Vista, near Santa Cruz, Bolivia (Steinbach); type in Cornell Univ., paratype M. C. Z. no. 26241.

Psammochares cymocles spec. nov.

Female. Black, but dark blue nearly all over, wings almost black, iridescent, somewhat violaceous; hind wings pale; spurs black.

Clypeus two and one-half times as broad as long, faintly concave

in middle below, hairs above as well as below; face but slightly narrowed above, front and vertex densely long-haired, basal joint of antennae hairy below, vertex-width very much longer than third antennal joint; ocelli in low triangle, hind ones about one and one-half times as far from eyes as from each other; pronotum weakly angulate behind, densely clothed with long black hairs; pleura hairy; propodeum very short, from side evenly rounded, with much long hair above.

Abdomen with hairs on basal part of first segment above, tip with a few stiff bristles; venter with few hairs, more numerous on last segment.

Legs have fine hairs above and below on all femora, three comb-spines on basitarsus, scarcely reach next, mid and hind tibiae with rather long spines, inner spur of hind tibia reach about to middle of basitarsus; claws toothed.

In the fore wing the marginal cell is more than its length from wing-tip, about as broad as the second submarginal cell, latter only a little longer than broad below, but above much shorter, receiving the first recurrent vein at tip; third submarginal about as long below as second, but much narrowed above by curving and sloping end-vein, receiving the second recurrent (slightly curved) a little beyond middle; extension of medius fully as long as the third submarginal cell; basal vein interstitial with transverse, in hind wing anal vein ends at forking of cubitus.

Length of fore wing 10.5 mm. to 11.5 mm.

From La Quinca, Argentina, 13 February (Harris). Type in Cornell Univ., paratype M. C. Z. no. 26240. Males from Cosquin, Sierra de Cordoba, 1–9 March (Cornell Exped.) and La Paz, 10 December (Joergensen), both Argentina. These, like the females, have the head very hairy and hairs on under side of basal joint of antennae, also fine hairs on femora; venation generally similar, the second submarginal a trifle longer, the wings are plainly paler than in female and show a broad darker band beyond the cells; body bluish as in female; inner spur of hind tibia a little more than one-half of the basitarsus.

Fore wing 7.5 mm. to 11.5 mm.

Psammochares allorices spec. nov.

Female. Body black, blue iridescence, in some views almost green, particularly the abdomen; mid and hind tibiae greenish, spurs black; fore wings pale brownish, rather darker before tip, hind wings scarcely

darkened except near veins and near tip. Head above densely long-haired; pronotum with long but not so dense hair; propodeum with long hairs above, pleura and basal part of first segment of abdomen above with shorter hair; a few long, fine hairs on all femora above.

Clypeus nearly three times as broad as long, below truncate; face broad but little narrowed above, vertex-width a little longer than third joint of antennae, hind ocelli only a trifle nearer to each other than to eyes; pronotum arcuate, scarcely angulate behind; propodeum short, from side rather low and evenly convex above, on the posterior slope is a jet black spear-mark, with the point forward.

Basal segment of abdomen large and broad, at tip with rather long slightly bristly hairs; venter with long hairs on all segments, many on first segment. Legs with few, rather short and widely separated spines on tibiae, inner spur not one-half of basitarsus, claws toothed, front basitarsus with three long comb-spines, the last about three-fourths of second joint.

In fore wings the marginal cell is a little less than its length from wing-tip, hardly as broad as third submarginal; second submarginal cell only a little longer than broad, basal side bent, receiving the first recurrent nearly one-fifth before tip; third submarginal cell longer and larger than second, end oblique and curved, receiving the second recurrent (curved in middle) at about middle, extension of medius about one-half the length of third cell; basal vein barely before transverse; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 11 mm.

From Mendoza, Argentine (Reed). Type at Cornell Univ.

Psammochares vestoris spec. nov.

Female. Black; wings somewhat yellowish brown, veins black; hind wings paler, spurs yellow-brown. Clypeus about three times as broad as long, truncate below, a few long bristles below middle; face a little narrower above, vertex-width as long as third antennal joint; front and vertex with moderately long hair; lateral ocelli a little nearer each other than to eyes; pronotum weakly angulate behind, shoulders not elevated, short and fine hair on shoulders and shorter in front; pleura bare; propodeum (from side) evenly rounded, with moderately long hair above.

Abdomen rather elongate, last segment above with numerous stiff bristles just before tip, sides and venter with long hairs, other

ventral segments scarcely hairy. Legs fairly long, front basitarsus with three comb-spines, neither first nor second reaching the next; mid and hind tibiae with long and stout spines, some above about width of joint, inner spur hind tibia reaching beyond middle of basitarsus, claws with sharp tooth near middle.

Fore wing with marginal cell hardly its length from wing-tip, scarcely broader than second submarginal cell, latter a little longer than broad, base curved and oblique, receiving the first recurrent a little before tip; third submarginal much longer below than second, narrowed more than one-half above, end oblique and curved, receiving the second recurrent (nearly straight) plainly beyond middle; extension of medius about one-third the length of third cell; basal vein interstitial with transverse; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 12.5 mm.

From Joinville, Santa Catharina, Brazil (Bequaert). Type M. C. Z. no. 26232.

Psammochares atrimene spec. nov.

Female. Body black with blue iridescence, in some views purplish, legs black, femora somewhat purple, wings brown, veins black; discoidal cells somewhat paler. Clypeus about two and one-half times as broad as long, lower margin plainly a little concave in middle. Head, thorax, pleura, propodeum, and basal segment of abdomen above hairy, dense on head and pronotum, rather long especially on propodeum and pleura; face only a little narrowed above; antennae long and slender, the third joint a little longer than vertex-width; hind ocelli about as far apart as from eyes; pronotum slightly angulate behind; propodeum short, from side evenly rounded; first segment of abdomen broad and high, venter with a few fine hairs, tip above with a few very small but bristly hairs. Legs moderately slender, front basitarsus with four long, slightly curved comb-spines, the last about two-thirds of second joint; hind tibia with a few rather short widely separated spines, inner spur black, about one-half of basitarsus; claws toothed.

In the fore wings the marginal cell more than its length from wing-tip, very broad at upper end of third cell, the outer side scarcely curved, broader than submarginals; second submarginal cell much longer than broad, base very oblique, receiving the first recurrent vein a little before tip; third submarginal much shorter below and

very much narrowed above, outer side strongly bulging outward, receiving the second recurrent (oblique) close to middle; extension of medius longer than third cell; basal vein interstitial with transverse; in hind wings anal vein ends at forking of cubitus.

Length of fore wing 11 to 12 mm.

From Mendoza, Argentine (Reed). Type at Cornell Univ., paratype at M. C. Z. no. 26242.

What may be the male is black, hair on head shorter, long hair on propodeum, short on basal segment of abdomen, spines on hind tibia as in female, inner spur a little more than one-half of basitarsus, claws cleft, venation much as in female, but marginal cell rather longer.

From Cosquin, Sierra de Cordoba, Argentine, 1–9 March (Cornell Exped.).

PSAMMOCHARES HOLMBERGI spec. nov.

This greatly resembles *P. separatus* Taschenberg, but the first and second segments are not margined behind, the first and most of second rufous below, and the third submarginal cell is not triangular. The clypeus is silvery, truncate below; face less silvery, a little narrowed above; second plus third antennal joints about equal vertex-width; lateral ocelli about as near each other as to eyes; few hairs on face and two long ones on vertex; pronotum angulate behind, short, and evenly sloping to collar, a short whitish line in front of each fore wing, pleura and coxae somewhat sericeous, and silvery each side of postscutellum; propodeum short, median groove on basal half, posterior slope moderately steep, hairs above short; abdomen widest near end of second segment, tip with stiff, sloping bristles, fifth and sixth segments with a few hairs, below hairy toward tip; legs with three short comb-spines on basitarsus, each more than length apart; hind tibia with about four spines in each row above, inner row slightly longer spines; inner spur about one-half of basitarsus. Marginal cell about one and one-third its length from wing-tip, fourth abcissa not one-half the costal length, scarcely as broad as second submarginal cell; latter a little longer below than broad, narrowed more than one-half above, receiving the first recurrent about one-third before tip; third submarginal cell scarcely longer below than second, narrowed nearly one-half above, outer side straight, receiving second recurrent (weakly curved) at middle, tip fully twice its lower length from margin of wing; in hind wings anal vein ends barely beyond forking of cubitus.

Length of fore wing 9.5 mm.

One female from Vicross, Minas Geraes, Brazil (Hambleton coll., Cornell) and another from Villarica, Paraguay, February (Schade coll. Cornell). Type at Cornell Univ., paratype M. C. Z. no. 26673.

The wings are pale fuscous, darker beyond cells, nearly hyaline in third discoidal cell.

Psammochares virilis spec. nov.

Body, legs, antennae black, first segment of abdomen rufous above except base, second rufous except hind border, third rufous on basal half; wings almost black, shining, basal cells partly pale, and a pale band just beyond third cell and across over the second recurrent vein. Head with few hairs, short ones on pronotum, none on pleura, short hair on propodeum.

Clypeus nearly truncate below, face plainly narrowed above, second plus third antennal joints a little longer than vertex-width; lateral ocelli as near to eyes as to each other; pronotum not deeply emarginate behind, but angulate in middle, nearly evenly sloping toward collar; propodeum hardly as long as broad in front, narrowed a little behind, posterior slope somewhat concave in middle; abdomen broadest on second joint, its sides parallel, basal segment almost as long as broad behind, last segment above with sloping, stout bristles, a few hairs on fifth and sixth segments, little hair on venter except near tip. Legs rather short, comb-spines short, three on basitarsus, little longer than width of joint, hind tibia with two rows of spines, outer of five or six, inner of four; inner spur of hind tibia fully one-half of basitarsus.

In fore wings the marginal cell is elongate and about its length from the wing-tip, fourth abscissa hardly one-third of costal length of cell, not quite as broad as the second submarginal cell, latter little longer below than broad, narrowed fully one-half above, receiving first recurrent near tip; third submarginal cell a little longer below than second, and also above, narrowed less than one-half above, outer side nearly straight, receiving the second recurrent vein (strongly curved) at middle, tip of cell about twice length from margin of wing; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 11 mm.

One female from Nova Teutonia, Santa Catharina, Brazil, 29 December (Plaumann). Type M. C. Z. no. 26671. This species is closely related to *P. holmbergi*; it differs in having the first and second

segments bordered behind with dark, the fore wings much darker, the face more narrowed at vertex, the hind ocelli further apart, and the median line on propodeum shows only near base. The venation is about the same, especially the third submarginal cell.

PSAMMOCHARES PERUVIANA spec. nov.

Body, legs, antennae deep black, in some views with bluish on body and femora, second and third segments of abdomen with a broad rufous band above, leaving a narrow black band with a median projection on the hind border of segment, fourth and fifth segment somewhat bluish; wings dark brown, somewhat paler behind marginal cell. Body very hairy; face with long hair, some equal basal joint of antennae, pronotum also with long hair, but shorter on mesonotum, pleura and propodeum hardly as long as on head, shorter hairs on basal joint of abdomen even to the hind border; tip of abdomen with the normal stiff bristles; venter moderately hairy, a few hairs on femora above, front coxae with hairs fully half its length.

Clypeus nearly truncate below, faintly concave, face a little narrowed above, second plus third antennal joints not equal vertex-width, lateral ocelli very much nearer each other than to eyes, pronotum angulate behind, evenly sloping to collar; propodeum from side evenly curved; abdomen broadest near middle of second segment, first segment rather short; comb-spines of moderate length, three on basitarsus; spines above on hind tibia nearly equal width of joint, four in inner row, five or six in outer row, inner spur almost one-half of basitarsus.

In fore wings the marginal cell is a little more than its length from wing-tip, barely broader than second submarginal cell, latter a little longer than broad, receiving first recurrent vein close to end; third submarginal cell not much shorter below than second, almost triangular, outer side curved, receiving the second recurrent vein (scarcely curved) near middle, third almost three times its length from wing-margin; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 13 mm.

One from Victoria, Dept. Junin, Peru, July (W. F. Walsh). Puno, Peru, May (J. Soukup), Am. Mus. N. H.

Type M. C. Z. no. 26672; paratype at A. M. N. H.

Pompilus anthracinus Taschb. may possibly be the male of this species; he mentions the abdomen as "basi sericeo-rufa"; *peruviana*

female has the second and third segments rufous, but agrees in hairy head and basal antennal joint.

Psammochares boliviana spec. nov.

Head and thorax deep black, antennae and legs also, abdomen above and below rufous to tip; wings brown, scarcely paler near tip, veins black; few hairs on head, very short on pronotum, a little longer on propodeum, last segment above with the stiff sloping hairs, much finer below, and a few on venter.

Clypeus slightly concave in middle below, sides broadly rounded, face but little narrowed above, median groove distinct, third antennal joint very long, nearly equal to vertex-width; anterior ocellus large, laterals a little nearer each other than to eyes; pronotum angulate behind, sloping evenly in front; propodeum slightly broader than long, sides somewhat rounded, no median groove, from side evenly curved to tip; abdomen broad on base, second segment a little broader than first, last nearly flat above, with marginal ridge. Legs rather short, comb-spines long, four on basitarsus; hind tibiae with two rows of spines above, each of about six, inner row longer spines, inner spur fully one-half of basitarsus.

In fore wings the marginal cell about one-fourth more than length before wing-tip, but little broader than second submarginal cell, latter not quite twice as long below as broad, base curved, receiving the first recurrent vein near tip; third submarginal cell plainly shorter below than second, narrowed fully three-fourths above, receiving the second recurrent vein (straight) at middle, tip of third cell more than twice its length from wing-border, in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 13 mm.

One female from Santa Cruz, Bolivia (J. Steinbach). Type M. C. Z. no. 26670.

Psammochares platensis Bréthes?

This was described from Uruguay; three females from Montevideo (Cornell Univ. coll.) and two from Maldonado, Brazil (Carey coll., Thayer Exped.) agree in many ways with the description, but they are all larger. Bréthes says nine millimeters; the smallest before me is eleven and one-half millimeters; he also says three comb-spines on the basitarsus; these have four, but in most of them the basal one is shorter, than others, and a small specimen might have it too short

to be counted. The description will also fit *P. semicincta* fairly well, and this has but three comb-spines on basitarsus; however *semicincta* is not uncommon in Argentine so he doubtless knew it. These specimens have the hair on face hardly one-half as long as in *semicincta*; no bluish on abdomen; the third submarginal cell is sometimes a little longer than the second, in all the top of third is shorter than that of second, but sometimes not much shorter. The pronotum behind is angulate, but not as strongly so as in *semicincta*. I surmise that these specimens are what Lepeletier called *P. tropicus* Fabr. but they are not the *tropicus* of Fabricius.

Psammochares veranes spec. nov.

Female. Body black, except a fairly large white or creamy spot on each side of second abdominal segment before middle; in some views the black of body shows a bluish or greenish iridescence; antennae, and legs black; wings dark brown, veins black. Head densely short haired, scarcely longer hair on vertex or behind, basal antennal joint with a few short hairs; pronotum with much short hair, above and on sides, mesonotum and pleura sparsely haired; propodeum densely hairy, hairs nearly twice as long as those on face; first segment of abdomen hairy above, tip of abdomen hairy, mostly on sides, a few stout, short bristles just before tip, venter slightly hairy; mid and hind femora with a few very short, fine hairs, their coxae hairy below, front coxae more hairy in front and behind.

Clypeus nearly three times as broad as long, lower edge truncate, with four long bristles on lower part; face scarcely narrowed above, frontal line faint, vertex not arched, plainly longer than second plus third antennal joints, antennae short, not reaching base of fore wings, third joint fully one-half longer than fourth; ocelli in a rather broad triangle, hind ones much nearer each other than to eyes; pronotum sharply angulate behind; propodeum, from side, strongly curved, median furrow indistinct, posterior slope with a rounded depression; abdomen broader than high, slightly flattened above.

Legs shorter than usual; front tarsi with a comb of long spines four on basitarsus, last two one-half length of joint; mid tibia slightly swollen, mid and hind tibiae with scattered, fairly long spines; inner spur of mid tibia three-fourths, of hind tibia two-thirds, of basitarsi.

Wings moderately short; in fore wings the marginal cell about its length from wing-tip, subtriangular, nearly one-half as broad as long, last abscissa long, slightly out-curved; second submarginal cell nearly

as broad as long below, base slightly curved, receiving first recurrent vein at last fourth; third submarginal cell no longer below than second, outer side curved and sloping to make cell nearly triangular, the second recurrent ends near or slightly beyond middle; basal vein ends at transverse; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 9 to 10 mm., body 10 to 11 mm.

From Itanhaem, Sao Paulo, Brazil, November (J. Lane). Type M. C. Z. no. 26632.

I have described this as a new species although I think it is the *Pompilus bilunatus* of Saussure; the name *bilunatus* is preoccupied by Haliday for an allied species. Saussure's name has been placed as a synonym of *semicinctus* Taschenberg, the latter however is quite different, much larger (15 mm.) with much more blue on both head and abdomen, and the abdomen somewhat flattened, with two large semicircular rufous spots across base of second segment and only narrowly separated, while this species has the creamy spots on the sides and so widely separated.

Psammochares pulchrisoma spec. nov.

Female. Black; abdomen with first and second segments rufous above and below, but with a dark apical border, third segment rufous on basal half above; face with golden above base of antennae, a streak behind each eye, a rather broadly interrupted band on hind border of pronotum, mesopleura, postscutellum, and a spot each side, and an elongate spot on each side of propodeum leaving a less broad black streak in middle, all more or less golden. Wings nearly evenly dark brown, veins black.

Clypeus very slightly emarginate in middle below; face plainly narrowed above; second plus third antennal joints plainly longer than vertex-width; ocelli in low triangle, hind ones about as near eyes as to each other, pronotum angulate behind. Propodeum much as in *inaurata*, but median groove is hardly as distinct; front basitarsus with comb of three moderately long, pointed spines; inner spur of hind tibia one-half of basitarsus; tibiae and basitarsi spined much as in *inaurata*.

In fore wings the basal vein ends at transverse, other venation much as *inaurata*. Little hair on body except at tip of abdomen, some on fourth segment above, and on front coxae.

Length of fore wings 12 to 14 mm.

From Province Sara, Bolivia (Steinbach). Type M. C. Z. no. 27137.

Psammochares argelesia spec. nov.

Head and thorax, legs and antennae black; abdomen rufous on three segments above and below, beyond black, wings dark brown, veins black. Clypeus and face from middle down with silvery pile, also occiput and back of eyes, white also on collar and a narrow stripe along hind border of pronotum, plainly interrupted in middle; hind border of mesonotum narrowly white, and yellowish each side of scutellum and postscutellum.

Lower margin of clypeus slightly, evenly concave, no hairs (except median pair of bristles), and none on face, a few on vertex, and some very short ones on propodeum, else thorax and propodeum without hair; front coxae with a few hairs on upper third.

Face moderately broad, median line complete; ocelli in moderately low triangle, hind ones a little nearer each other than to eyes; antennae quite slender, third joint fully equal to vertex-width. Propodeum as in allies, trace of groove near base; abdomen broad at base, slightly flattened; legs with moderately long spines; front basitarsus with three comb-spines, the first long and more than its length from base; both mid and hind femora with short spines on apical half above, these tibiae with long, stout spines, inner spur of hind tibia fully half of basitarsus.

In fore wings the marginal cell rather long and about its length from wing-tip, broadest at top of third submarginal cell; second submarginal nearly one and one-third as long below as broad, little narrowed above, receiving the first recurrent vein near tip; third submarginal cell about as long below as second, above only about one-third of lower length, both ends sloping, outer curved, the second recurrent vein (nearly straight) ends a little beyond middle; the cubitus almost reaches margin of wing; the base of third discoidal cell is oblique; in hind wing the anal ends a little beyond forking of cubitus.

Length of fore wings 14.5 mm.

One female from Belem, Para, Brazil, May (F. X. Williams). Type M. C. Z. no. 27136.

Related to *pulchrisoma*, but the rufous segments are not margined behind with dark, the second submarginal cell much longer, the third antennal joint longer, and no distinct silvery or golden spots on the pleura; also separated from *turcia* by the lack of these spots.

Psammochares decepta Fox (Pompilus)

A paratype from Chapada, Brazil (H. H. Smith), April; and Urucum, Corumba, Brazil, 23 to 29 December (Cornell Exped.).

Psammochares partita Fox (Pompilus)

From Province Sara, Bolivia (Steinbach); Cosquin, Sierra de Cordoba, Argentina 1–9 March (Cornell Univ. Exped.); Zanderji, Boven, Para Distr., Surinam, 21 April (Cornell). Chapada, Brazil (H. H. Smith).

Psammochares hermanni Holmb. (Pompilus)

From La Paz, 19 December, Argentina (Joergensen); Mendoza, Argentina, 26 December (Joergensen); Patrerillos, Mendoza, Argentina, 16 to 20 March, 4,000 ft. (Cornell Exped.).

Psammochares semicincta Dahlb. (Pompilus)

From Mendoza, Argentine, 8 January (Joergensen); La Paz, Argentine, 19 December (Joergensen); La Quiaca, Argentina, 13 February (Cornell Exped.). Described from Brazil. *Pompilus bilunatus* Sauss. is not the same; it has whitish spots on side, not above, a long comb, and very hairy body.

Psammochares arequepensis Bréthes

Three females from Santa Cruz, Bolivia (Steinbach), also Buenavista near Santa Cruz, Bolivia (Steinbach, Cornell coll.).

Psammochares alcataria Banks

Described from Kartabo, British Guiana; Paramaribo, Surinam, and La Cumbre, Colombia.

Psammochares bilunata Haliday (Pompilus)

Both sexes have been taken at Cordova, Argentine (W. M. Davis) and at Cosquin, Sierra de Cordoba, Argentina, 1 to 9 March (Cornell Univ. Exped.). Described from Maldonado, Brazil.

What I consider the female of *bilunata* fits fairly well to *P. arechavaletai* of Brèthes.

Psammochares turcica Febr. (Pompilus)

Two females from Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert). The male, like female, is very close to *P. personata*, but is less slender and has the hind tibiae black.

Psammochares echinata Fox (Pompilus)

From Kartabo, Bartica, Demerara River, all British Guiana, January to October; Muzo, Dept. Boyaca, Colombia, 900 m., July, (Bequaert); Maracajú, Matto Grosso, Brazil, April-May (Fairchild); and Santa Cruz, Bolivia (Steinbach); Rio de Janeiro (H. H. Smith).

Psammochares ornamenta Fox (Pompilus)

Known only from males; described from Brazil; specimens from Bartica, Kartabo, and Essequibo River, January to August; Chapada, Brazil (Smith), also from Belem, Para, Brazil (Wolcott).

Psammochares argenteomaculata Fox (Pompilus)

A female from Santa Cruz, Bolivia (Steinbach); described from Chapada, Brazil (H. H. Smith).

Psammochares marginicollis Taschb. (Pompilus)

One female from Villa Rica, Paraguay, January (Schade). It is a larger species than *insularis*, with deep black wings. It is possibly the *phaleratus* of Perty. Described from Argentine. Also one from Puerto Bermudez, Rio Pichis, Peru, 12 to 13 July (Cornell Exped.).

Psammochares inaurata Smith (Pompilus)

Specimens from Jatun Yacu, Rio Napo watershed, 700 m., Ecuador (MacIntyre), Santa Cruz, Bolivia (Steinbach); Villa Rica, Paraguay, February; and several places in Argentina, Mendoza, 28 March (Joergensen); Petrerillos, 23 February (Joergensen); La Rioja (Cornell coll.) and (A. M. N. H.), and Psao de 1. Libres, Corrientes, 12 to 14 January (Cornell coll.). Described from Cordova, Argentine.

Extremely similar to *marginicollis*, but wings dark brown, and not so large. *Pompilus insularis* Holmberg I believe is a synonym, or very nearly related.

Psammochares personata Fox (Pompilus)

Many males from Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert), also Belem, Para, Brazil (Wolcott). Described from Corumba and Santarem, Brazil.

Several females taken at same time and place are similar to *torquata*, but smaller.

Psammochares separata Taschb. (Pompilus)

From Cosquin, Sierra de Cordoba, 1 to 9 March (Cornell Univ. Exped.); La Rioja, Argentine (Giacomelli); described from Argentine. The male has the secondary sexual characters as in Notiochares.

Psammochares caloderes Banks

Described from Restrepo, Dept. Meta, Colombia.

Psammochares inculcatrix Cameron (Pompilus)

From St. Augustine, Trinidad, July (Weber); Ongelijk, Surimam, May (Cornell); El Campamiento, Col Perene, Peru, June (Cornell Univ. Exped.). Male is like a Notiochares.

Psammochares scalaris Taschb. (Pompilus)

From Maldonado, Brazil (Carey, Thayer Exped.), and Cosquin, Sierra de Cordoba, Mendoza, 4,000 ft., 16 to 20 March (Cornell Exped.). Smith's *Pompilus representans* appears to be a synonym.

Psammochares taschenbergi Bréthes

Many males from Santa Cruz, Bolivia (Steinbach); La Rioja, Argentine, (Giacomelli, Cornell); and Pirapona, Minas Geraes, Brazil, 11 to 13 November (Cornell Exped.). Also Buenavista near Santa Cruz, Bolivia (Steinbach) (Cornell). Greatly resembles *personata*.

Psammochares triquetra Fox (Pompilus)

From Guayaquil, Ecuador, May, June (C. T. Brues); Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert); Urucum,

Corumba, Brazil (Cornell); La Rioja, Argentina (Giacomelli, Cornell); Villa Rica, Paraguay, December, (Cornell), Belem, Para, Brazil (Wolcott). Described from Chapada and Corumba, Brazil.

Pompilinus Ashmead

The propodeum is bare; the marginal cell short, triangular, and remote from tip of wing; the third submarginal cell triangular or nearly so and often petiolate; the comb of the female is of very short spines; the tip of the abdomen has some stiff bristles.

1. Females 2
   Males 3
2. Abdomen completely rufous ..... *completus*
   Abdomen with two or three segments near tip black ..... *orthodes*
3. Pronotum with yellowish hind border; face, pleura, coxae sericeous ..... *vespuccii*
   Pronotum entirely black, as also rest of thorax, no sericeous on pleura, coxae, nor face ..... *lynchii*

Pompilinus vespuccii Dalla Torre

Head and thorax deep black, shining, lower face and clypeus silvery, hind border of pronotum pale yellowish, abdomen above red on more than apical half of first segment, all of second, and basal half of third, beyond and on venter black; legs wholly black, spurs dark; antennae dark brown, but beneath mostly rufous; fore wings nearly evenly pale brown, veins and stigma black, hind wings nearly hyaline.

Clypeus rather evenly rounded below from eye to eye, fully twice as broad as long; antennae thick, from below joints four, five, and six are each not twice as long as broad, front from side convex between eyes, face narrowed near vertex, from in front vertex slightly convex; ocelli small, in low triangle, hind ones much nearer each other than to eyes.

This is the *Pompilus tricolor* Taschenberg, but *tricolor* was preoccupied.

Specimens from San Juan, Argentine; Villa Alegre, Rio Branco, Amazonas, Brazil. Only the male known.

Pompilinus completus spec. nov.

Female. Head, thorax, propodeum, legs and antennae dark brown, abdomen dull rufous above and below, extreme base black, covered

with a slight whitish bloom; wings pale brown, hind wings only slightly brownish.

Clypeus more than three times as broad as long, lower margin broadly and rather deeply concave, with a pair of bristles below middle; face scarcely narrowed above, vertex broader than antennal joints two plus three; ocelli in a low triangle, hind ones nearer each other than to eyes; frontal groove complete, a few short hairs on vertex.

Pronotum curved and sloping in front, angulate behind, bare; propodeum about as broad at base as long, from side evenly rounded, faintly flattened on posterior slope, no distinct median line.

Abdomen rather broad at base, a trifle flattened; legs of moderate length, tibiae and basitarsi with fairly long spines, inner spur of hind tibia one-half of basitarsus.

In fore wings the marginal cell much more than its length from tip of wing, subtriangular, broader than submarginal cells; second submarginal cell rhomboidal, about as long as broad, receiving first recurrent vein near end; third submarginal cell about as long below as second, outer side curved, top very short, receiving second recurrent vein near middle; basal vein ends at transverse, in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 8 mm.

From La Rioja, Argentine (Giacomelli); type at Cornell Univ., paratype M. C. Z. no. 26077.

Pompilinus orthodes Banks

From Rio Frio, Magdalena, Colombia, 8 December (G. Salt); Sevilla, Magdalena, Colombia, 15 June (G. Salt); St. Augustine, Trinidad, 10 June (N. A. Weber); Kartabo, July, Georgetown, 29 September, both British Guiana.

Pompilinus lynchii Holmb. (Pompilus)

From Mendoza, Argentine; and Cruz de Pledra, Mendoza, 14 March, Argentine. Only the male is known.

Notiochares Banks

In general very similar to Psammochares, but with a distinct emargination in middle of lower border of clypeus, this emargination does not reach to sides. In the males there is a small patch of velvety

hair on the hind margin of the fourth ventral segment, and the subgenital plate is incised at tip; both these characters occur in several species of Psammochares that do not have the clypeal emargination, and they may belong to Notiochares, if some character can be found in the female.

Table of species

1. Males 2
   Females 4
2. The median carina of subgenital plate reaches almost to base of apical fork, lateral carina long and somewhat curved; no white hair back of head or white line across collar, coxae beneath scarcely sericeous ..... *amethystina*
   Lateral carina much shorter and not curved 3
3. Median carina nearly complete, lateral extremely short and divergent, tip of plate deeply indented; no white hair nor pubescence back of head ..... *pisoensis*
   Median carina fading out before middle, laterals longer than in *pisoensis* and more nearly parallel to median; white hair and pubescence back of eyes and on collar; coxae beneath strongly sericeous ..... *coxalis*
4. Pronotum behind arcuate, propodeum with rather long fine hair; no indication of median groove, three comb spines on basitarsus; third submarginal cell a little longer than second; inner spur more than one-half of basitarsus ..... *diffinis*
   Pronotum angulate behind; propodeum at most with very short hairs, usually four comb spines on basitarsus; third submarginal not longer, usually plainly shorter than second; inner spur shorter 5
5. Back of head and collar without any white hair or pubescence, not at tip of propodeum, coxae little if any sericeous beneath, venter, as elsewhere strongly blue ..... *amethystina*
   Back of head plainly with white hair, and white pubescence back of eyes and a line across collar, also narrow band across tip of propodeum; coxae, especially the mid and hind ones, strongly sericeous 6
6. Propodeum silvery only near tip; no sericeous bands on abdomen ..... *coxalis*
   Propodeum entirely silvery above; a band of silvery pubescence across base of second and third segments *Psammochares caloderes*

Notiochares amethystina Fabr. (Pompilus)

A species of Psammocharid common in northern South America is plainly blue on body and the wings have a strong blue iridescence. This I take to be *Pompilus amethystinus* Fabricius; I know of no other species in this region which fits the description so well.

Before me are over fifty specimens from Colombia to Surinam, half from British Guiana. Others are from the Amazon valley, Matto Grosso, Paraguay and from Central Peru. Twelve females and seventeen males from Santa Cruz, Bolivia do not differ. I have examined many more.

The second submarginal cell is usually longer than the third, both above and below, but sometimes the third is as long below. The amount of narrowing of the third above varies (as in many species), but it rarely comes to a point. There are normally four comb spines on the front basitarsus; the last dorsal segment is usually more or less cinereous where the bristles are most numerous, the hairs on preceding segment can scarcely be called bristles. In the hind wing the anal vein usually ends plainly beyond the forking of cubitus, but sometimes only a trifle beyond; the inner spur of hind tibia is not more than one-half of basitarsus; the hind part of propodeum is somewhat flattened in middle. The males have the tuft of hair on hind border of the fourth ventral segment; the subgenital plate is more or less deeply emarginate at tip, but the part each side is never as acute as in *cubanus* or *pisoensis*; there is a median carina from base to tip, and each side of it another shorter carina running obliquely outward. Three females and two males from Banos, Ecuador, 1,600 to 1,900 m., do not seem to differ from typical specimens from Surinam.

Two males, however, from Guayaquil, Ecuador, do have the subgenital plate deeply triangularly incised and each point is sharply acute thus agreeing with Strand's *pisoensis*; so this may prove to be a good species.

Notiochares coxalis Banks

From Kartabo, British Guiana, July-August (Wheeler).

Notiochares diffinis spec. nov.

Black throughout, with blue iridescence on wings and on abdomen, less on thorax and head, not nearly so deep a blue as *amethystina*; second and third ventral segments sericeous, coxae less strongly

sericeous, more brown; clypeus with a rather rusty-brown pile; from above one sees a whitish pile on each lower corner of the face. Front with short hair in middle, propodeum with very fine hair, and on the sides longer, longer than in *amethystina*; last segment of abdomen above with many stiff, sloping bristles, few hairs on fifth segment above, venter with few long hairs.

Clypeus fully as deeply excavate as in *amethystina*, lateral ocelli much nearer each other than to eyes; vertex not as broad as in *amethystina*, and the third joint of the slender antennae is much longer than the vertex-width; propodeum much more evenly rounded, no separation of basal part from posterior slope, which is evident in *amethystina* and no indication of a median line. Abdomen and legs about as in that species, hind tibiae with two rows of six to eight spines above, inner spur more than one-half of basitarsus; comb-spines like those of *amethystina*, but only three on basitarsus.

In fore wings the marginal cell not its length from wing-tip, broader than the second submarginal cell, latter twice as long below as broad, narrowed one-third above, base oblique and slightly curved, receiving the first recurrent vein close to tip; third submarginal cell a little longer below than second, narrowed one-half above, this upper side nearly as long as that of the second, receiving the second recurrent (slightly curved) near middle; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 15 to 18 mm.

Two females from Iquitos San Rogue, Peru, March (Klug coll.). Type at Cornell University, paratype M. C. Z. no. 26699.

Aplochares Banks

Clypeus elevated, convex, lower margin with a deep rounded emargination in middle; female with a comb, spines slender; mid and hind tibia with slender spines; claws toothed; last joint of tarsus below with a few teeth in middle; wings tend to fold lengthwise as in Episyron; marginal cell not its length from tip of wing, basal vein interstitial with the transverse, thorax, pleura, and propodeum without hair; head bare, except two or three erect hairs each side on vertex; abdomen with fine hairs at tip; antennae slender. Type *Pompilus imitator* Smith. From Lophopompilus and Notiochares (which also have emarginate clypeus) by absence of stiff bristles at tip of abdomen, the folding wings, absence of hair on much of body,

and very long slope of the propodeum. In both species the third submarginal cell is very long.

Aplochares imitator Sm. (Pompilus)

One from Kartabo, British Guiana, 11 October; others from Restrepo, Dept. Meta, Colombia 500 m. (Bequaert); Santarem, Brazil (H. H. Smith); Mt. Duida, Venezuela, 13 November (Amer. Mus. Nat. Hist.).

Aplochares adrastes spec. nov.

Dull black, not shining; lower margin of clypeus, under side of basal joint of antennae, joints four, five, six, and often seven or part of eight, rufous, especially below; legs ferrugineus, the femora more or less black, tips of some tarsal joints dark; wings reddish brown, dark near base, gradually fading toward the nearly hyaline tip, not as dark as *imitator* and the tip is not white. Coxae beneath and hind coxae on the side sericeous, also the clypeus and lower corners of face. Clypeus with a few pale hairs near lower margin, a few hairs on vertex each side, and some small hairs on sides of propodeum, tip of abdomen with fine sloping hairs, also below, and a few on each ventral segment; front coxae with but two or three long hairs.

Clypeus with a rounded emargination in middle of lower margin; face with distinct frontal groove; lateral ocelli a little nearer each other than to eyes; third antennal joint very long, slender, and curved, fully equal to the width of vertex. Pronotum very short, almost wholly front, very faintly arcuate behind; propodeum sloping from near base, a slight median depression on base; abdomen and legs like *imitator*, three comb-spines on basitarsus, of moderate length.

Venation similar to *imitator*, in fore wings the marginal cell less than its length from wing-tip, as broad as the submarginals, last abcissa slightly concave on outer side; second and third submarginals about equal in length below, third usually more narrowed above, first recurrent vein ends near apical third or fourth of cell, second recurrent (curved and almost sinuous) ends a little beyond middle (not as much so as in *imitator*). In hind wings the anal vein ends at forking of cubitus.

Length of fore wing 9 to 12 mm.

Four females from Nova Teutonia, Santa Catharina, Brazil, 24 January, 8, 23 February (F. Plaumann).

Type M. C. Z. no. 26703.

A male, same locality, 24 December, has clypeus broadly truncate below, with a narrow rufous border; the ocelli in a broader triangle; antennae with under side of first joint and much of the third yellowish, the hind margin of pronotum narrowly yellowish; femora brown on base, rest of legs dull yellowish as female. Propodeum more rounded than in female, with much fine hair above. Venation as in female. The subgenital plate is narrowed and rounded at tip, with much fine and very short hair, no carina. Antennae much like Notiochares, but scarcely tapering toward tip, and apical joints not as long.

Length of fore wings 8 mm.

Anoplius Lepeletier

This genus is very similar to Psammochares, but lacks the comb on front tarsus, the tip of abdomen the same; the propodeum is usually shorter. The males have a ventral brush of hair.

Table of females

1. Last three segments of abdomen above plainly cinereous; second submarginal much longer than broad ..... *davisi*
   All segments black or bluish 2
2. Clypeus slightly convex on lower margin, this margin continuing the curve of the sides, more or less covered with whitish pubescence; second plus third antennal joints longer than vertex width; abdomen shining blue black; second submarginal cell longer below than broad ..... *mundulus*
   Lower margin of clypeus truncate 3
3. Clypeus three times as broad as long; second submarginal cell but little longer below than broad; third abcissa of radius nearly as long as second, body bluish; second submarginal cell usually little if any longer than broad 4
   Clypeus not three times as broad as long; second submarginal cell plainly longer below than broad; third abcissa one-half as long as second, often still shorter; second plus third antennal joints equal to vertex width 5
4. Second plus third antennal joints plainly shorter than vertex width; clypeus more than three times as broad as long; front basitarsi with all spines very short; smaller and less hairy species 7

Second plus third antennal joints more nearly equal to vertex width; clypeus scarcely if any more than three times as broad as long; front basitarsi have a few spines longer than width of joint; larger and more hairy species, some hairs on front femora 6

5. Body above bluish; wings violaceous; ocelli in a moderately broad triangle ..... *amarus*
   Body black, rather slender; wings coppery; ocelli in a narrow triangle ..... *angustus*

6. Front and vertex strongly and mostly transversely ridged; head, thorax and abdomen densely long-haired, some hairs on basal antennal joint ..... *perpilosus*
   Front and vertex only microscopically striate, hair on head and thorax not as dense nor as long ..... *bolivari*

7. Inner spur more than one-half of hind basitarsus ..... *williamsi*
   Inner spur hardly one-half of hind basitarsus ..... *minor*

Anoplius bolivari Banks

Females from Vista Nieve, Santa Marta, Colombia (Salt); and Vista Nieve, San Lorenzo Mt., Colombia (Bequaert).

Anoplius perpilosus spec. nov.

Body black, with a general bluish tinge over much of body, especially on abdomen above. Wings dark brown with a bluish iridescence, veins black.

In general much like *A. bolivari*, but head, thorax, and propodeum are more densely haired, and with longer hairs, some on front femora, and also on basal antennal joint; hair above on basal segment of abdomen nearly twice as long as in *bolivari*.

Clypeus fully as broad as in *bolivari*; ocelli in a broader triangle, the hind ones nearer each other than to eyes. The front and vertex are covered with very distinct (with lens) irregular but mostly transverse ridges; much coarser than the fine microscopic sculpture of other species; vertex a little broader than in *bolivari*, the second plus third antennal joints not quite equal to vertex-width. Spination of legs very similar, but on tibiae and basitarsi not as long as in *bolivari*, the inner spur of hind tibiae a little more than one-half of basitarsus.

Venation similar to *bolivari*, the marginal cell a little longer, the second submarginal about as long below as broad, the third more narrowed above than in *bolivari*, the second recurrent vein ends plainly beyond middle.

Length of fore wings 12 mm.

One female, probably from Bogota, Dept. Cundimarca, Colombia, 2600 m. (Amer. Mus. Nat. Hist.).

Anoplius mundulus Fox (Pompilus)

Described from Chapada, Brazil, I have one from Mera, Ecuador, 23 January (F. X. Williams).

Clypeus slightly rounded below, not three times as broad as long; antennae long and slender, third joint equal to vertex width; ocelli in a moderately broad triangle; marginal cell rather short; first recurrent is plainly curved above, ends near tip of cell; third submarginal cell about as long below as second, but third abscissa hardly one-half of second, second recurrent ends before middle.

Anoplius davisi spec. nov.

Female. Black, clypeus and lower face cinereous, abdomen above with faint bluish sheen, segments four, five, and six plainly cinereous above and below, spurs yellowish brown; wings brown, veins black.

Clypeus nearly three times as broad as long, faintly concave below, a few long hairs in the row below middle; face a little higher than broad, somewhat narrowed above, median groove distinct, a few short hairs near eyes and on vertex, vertex-width much longer than third antennal joint; lateral ocelli rather widely separated, but a little nearer each other than to eyes; pronotum angulate behind, a few hairs on shoulders; pleura almost bare; propodeum short, evenly rounded, a trace of a median groove, above with moderately long hair; no hair on basal segment of abdomen, last segment with long hairs above and near tip a group of very stout bristles, sides with long hair, a few on ventral segments.

In fore wings the marginal cell is about its length before wing-tip, as broad as submarginals; second submarginal cell rhomboidal, a little longer than broad, receiving the first recurrent vein close to tip; third submarginal cell shorter and much narrowed above, outer side curved, receiving the second recurrent (scarcely curved) at middle; extension of medius nearly as long as the cell; the basal vein interstitial with transverse; in hind wings the anal vein ends a little beyond forking of cubitus.

Length of fore wing 11 mm.

From Cordova (Davis). Type M. C. Z. no. 26235.

ANOPLIUS ANGUSTUS spec. nov.

Female. Black, without bluish; wings blackish on basal part, paler toward tip and on hind wings; spurs black. Body rather more slender than usual; clypeus about two and one-half times as broad as long, lower margin straight, a few bristles across below middle; face much higher than broad, somewhat narrowed above, with moderately long hairs on vertex, and shorter each side by eyes; vertex-width almost as long as third antennal joint; ocelli in a narrow triangle, the hind ocelli hardly two diameters apart and much farther from the eyes. Pronotum angulate behind, short hairs in front and on shoulders; pleura not hairy; propodeum evenly curved, hairy above; a few small hairs above on basal part of first abdominal segment, tip above with rows of straight bristles, last ventrite with some long hairs, scarcely any elsewhere. Legs moderately long, front basitarsus with three short spines on outer side, mid and hind tibiae with spines above about one-half diameter of joint, inner spur fully one-half of basitarsus.

In fore wings marginal cell is a little less than its length from wing tip, fully as broad as the submarginals, the second submarginal longer than high, its basal vein bent near middle, receiving the first recurrent near apical third; third submarginal little if any longer, nearly triangular, outer side curved, receiving the second recurrent (nearly straight) a little beyond the middle; extension of medius fully one-half way to margin of wing; basal vein ends a trifle before transverse; in hind wings the anal ends at forking of cubitus.

Length of fore wing 10 mm.

From Nova Teutonia, St. Catharina, Brazil, 4 February (F. Plaumann). Type M. C. Z. no. 26236.

A male from the same locality, 4 February is a little shorter and much more slender than female; the fore wings are pale brownish, with a large hyaline spot over the discoidals and second and third submarginal cells; third submarginal cell shorter than in female; the fourth and fifth ventrites have a mass of erect hair in the middle; inner spur almost four fifths of basitarsus; pronotum shorter above.

ANOPLIUS AMARUS spec. nov.

Female. Blue black, shining, lower face with silvery pubescence each side of antennae and extending down over upper part of clypeus; wings rather pale brown, darker toward tip and with a reddish to violaceous iridescence, veins black, spurs brown.

Clypeus about two and one-half times as broad as long, lower edge straight in middle, convex on sides; face moderately broad, little narrowed above, with quite long hair, median groove distinct, vertex width about as long as third antennal joint; pronotum angulate behind, a few hairs each side, pleura bare; propodeum hairy above; base of first abdominal segment hairy above, straight bristles at tip of last segment, venter with few hairs, but more toward tip. Legs with spines on tibiae hardly one-half diameter of joint; front basitarsus with only very minute spines, inner spur of hind tibia only little more than one-half of basitarsus.

In fore wings the marginal cell almost its length before wing-tip, hardly as broad as width of second submarginal, latter rhomboidal, a little longer than broad, receiving the first recurrent vein near tip; third submarginal cell about as long below as the second, much narrowed above, outer side curved, receiving the second recurrent (slightly curved) a little beyond the middle; extension of medius about one-half length of cell; basal vein barely before transverse; in hind wing anal vein ends at forking of cubitus.

Length of fore wing 8 to 10 mm.

Type from Puerto Bermudez, Rio Pichis, Peru, 12–19 July (Cornell); paratypes from Blairmont, British Guiana, September, November (F. X. Williams), M.C.Z. no. 26753 and with Mr. Williams.

Anoplius williamsi spec. nov.

Female. Body black; abdomen bluish above, sometimes faintly on thorax; antennae and legs black; wings nearly evenly dark brown, but often paler behind the marginal cell over submarginal and third discoidal cells, hind wings paler brown in front, and still paler behind; stigma and veins nearly black; fore wings above violaceous. Clypeus more than three times as broad as long, with a few bristles above, lower margin truncate, face broad, somewhat higher than broad, but little narrowed above; vertex-width greater than second plus third antennal joints; frontal groove complete, ocelli in a small triangle, hind ocelli plainly nearer each other than to eyes, front and vertex with rather long erect hair; pronotum angulate behind, with shorter hair, pleura with scattered short hairs; propodeum nearly as broad at front as long, from side evenly convex, and with long hairs above, first segment with some short hair above near base; apical segment with stout bristles, a few hairs on fifth segment; venter sparsely hairy.

Legs about as short as usual, mid and hind tibiae with short spines above, inner spur of hind tibiae fully one-half of basitarsus.

In fore wings the marginal cell is more than its length from wing-tip, about as broad as the second submarginal cell, latter nearly as long below as broad, but narrowed above by the curved base, receiving the first recurrent vein a little before tip; third submarginal cell longer below than second and often shorter above, outer side curved, receiving the second recurrent vein (a little curved) near middle; basal vein ends a little before transverse; in hind wings the anal vein ends a little before forking of cubitus.

Length of fore wing female 8 to 8.5 mm.; male 6 to 7 mm.

From Mera, Ecuador, February, and Banos, Oriente, Ecuador, 27 December, 1 February (all F. X. Williams); also Tunguarhua, Banos, Oriente, Ecuador, 1,600 to 1,900 m. (W. C. MacIntyre). Type M.C.Z. no. 26754.

The male is black, with only a trace of blue; wings as in female, but marginal cell shorter, the third submarginal cell shorter above than second, and subtriangular. Head rather more hairy than in female, and basal antennal joint hairy below; antennae moderately thickened; abdomen slender, not hairy at tip; there is some erect hair, forming brushes, on third, fourth, and fifth ventrites, that on fourth and fifth much denser, and reaching nearly to side-margins; subgenital plate slender, with median ridge on basal two-thirds, beyond flattened, and densely short haired on tip, which is narrowed.

Anoplius minor spec. nov.

Body black, abdomen iridescent bluish, especially above, wings hardly as dark as in *williamsi*, but a broad dark apical part just beyond cells. Head with few but rather long hairs, much as in *williamsi*, little hair on pronotum, but propodeum with fine and fairly long hairs. Structure much as in *williamsi*, clypeus scarcely as broad, or rather a bit longer in middle, a row of four bristles on lower part, few hairs above; vertex broader than length of second plus third antennal joints, ocelli in rather narrow triangle, hind ones much nearer each other than eyes, frontal groove complete and distinct; pronotum rather sharply angulately emarginate behind; propodeum from side nearly evenly curved, no median groove; first segment of abdomen with few very faint hairs near base; legs not so long as in some species, the spines on hind tibiae very short; inner spur hardly one-half of basitarsus.

Venation much as in *williamsi*, third submarginal cell more nearly triangular, marginal cell more than its length from wing-tip, almost as broad as submarginals; second recurrent vein (evenly curved) ends close to middle of third cell.

Length of fore wings 6 mm.

Two females from Arequipa, Peru, October, 1937 (Carlos Nicholson); type in Amer. Mus. Nat. Hist., paratype at M.C.Z. no. 26058.

Anoplius varunus spec. nov.

Male. Head, thorax, propodeum, antennae and legs black; abdomen below yellowish rufous on first and second segments, above rufous on first (except base), second wholly, and basal part of third segment, beyond black until the sixth segment which is snow-white; pronotum bordered behind with white. Clypeus and lower half of face strongly silvery pubescent, also across lower front of pronotum, coxae and pleura also strongly silvery, apical part and sides of propodeum above silvery, less plainly in front; wings nearly hyaline, but dark in marginal cell and beyond the third submarginal cell; hind wings hyaline, paler brown broadly over tip.

Clypeus little more than twice as broad as long, not extending beneath eyes; face narrowed above, vertex nearly as broad as the length of the first plus second plus third antennal joints, a few very minute hairs on vertex, hind ocelli a little nearer to eyes than to each other; pronotum with white hair at collar, angulate behind; propodeum without hairs above, with a trace of median groove, low and nearly flat above; abdomen long and slender, base broad, the third ventral segment has some erect, black hair, on fourth and fifth segments this hair is dense and over the middle of each segment.

Legs slender, hind femora with spine-pits on apical half above, tibiae with spines above about equal to diameter of joint, inner spur three-fourths of basitarsus. In fore wings the marginal cell is about one and one-half its length from wing-tip, triangular; second submarginal about twice as long below as above, receiving first recurrent vein near middle; third submarginal triangular and short petiolate; the recurrent ends a trifle beyond middle, this cell more than three times its lower length from margin; basal vein interstitial with transverse; stigma very small and short, not equal to abscissa one, tip nearly truncate.

Length of fore wings 7 mm.

A male from New Amsterdam, British Guiana, August (F. X. Williams). Type M.C.Z. no. 27224.

Anoplius varius Fabr. (Pompilus)

A male from Sint Barbara Pln., Surinam Riv., Surinam, 11 April (Cornell coll.), agrees with the description in having the fourth segment of abdomen black while the first is broadly sericeous on base, second and third more narrowly on base, fifth wholly sericeous (at least part extended). The venter has second and third segments sericeous; the head and pleura are almost wholly sericeous; the pronotum all but a small black spot each side, posterior border strongly so, femora and tibiae also; the coxae and apical half of propodeum almost silvery; antennae black, the third and fourth joints below are rufous; the wings are mostly nearly hyaline, with a broad brown apical band a little beyond the cells, but occupying the marginal cell.

The fourth ventral segment has a brush of erect black hair on middle, and the fifth has some erect hairs but not forming a brush. Clypeus truncate below; pronotum strongly angulately incised behind; claws cleft, inner spur of hind tibia fully three-fourths of basitarsus.

In fore wings the marginal cell is nearly its length from wing-tip, hardly as broad as second submarginal cell, latter a little longer below than broad, narrowed fully one-half above, receiving the first recurrent beyond middle; third submarginal cell little longer below than second, narrowed more than one-half above, outer side nearly straight, second recurrent vein ends near middle; basal vein interstitial with transverse; in hind wings the anal vein ends at or very near forking of cubitus.

Length of fore wings 10 mm.

Fox records males from Chapada and Santarem, Brazil.

Neanoplius gen. nov.

Belongs to the Psammocharinae, and related to Anoplius. No comb of spines on front leg (two moderate spines on basitarsus, none at middle of second joint). Claws with a tooth in both sexes; only fine, curved hairs at tip of abdomen; antennae slender; basal vein in both sexes ends a little before transverse; marginal cell moderately long; in hind wing anal vein ends near fork of cubitus. Male without the ventral brush; the subgenital plate modified.

NEANOPLIUS COERULEOSOMUS spec. nov.

Female. Body blue, also femora, rest of legs and antennae black; wings pale brown, plainly darker over basal and transverse veins, a darker band beyond the cells, veins black; spurs black. Clypeus about three times as broad as long, below truncate, some hairs above as well as below; face a little narrowed above, front and vertex with rather long hair, vertex-width scarcely longer than third antennal joint, lateral ocelli much nearer each other than to eyes; pronotum angulate behind, hairy on shoulders; pleura partly hairy; propodeum short, nearly evenly rounded, with fairly long hair; first abdominal segment with short hair on sides of basal part, venter with a few hairs on each segment, last segment with a few long hairs each side, those above few and not especially stout.

Legs moderately long, all femora with a few fine hairs above, also a few below on mid and hind coxae, no spine at middle of second joint of front tarsus, but three small ones on the basitarsus; hind tibia with spines hardly one-half diameter of joint, inner spur hardly one-half of basitarsus, claws with tooth beyond middle.

Fore wings with marginal cell scarcely its length from wing-tip, outer section curved, broader than second submarginal cell, latter longer than broad, little narrowed above, both ends oblique, receiving the first recurrent a little before tip; third submarginal cell much longer below but no longer above than second submarginal, outer side but little curved, receiving the second recurrent (faintly sinuous) a little before the middle, extension of medius one-half of cell; basal vein ends a little before transverse; in hind wings the anal vein ends barely before the forking of cubitus.

Length of fore wing 12 mm.

From Nova Teutonia, Santa Catharina, Brazil, 23 February (Plaumann).

The male with more slender body which evidently belongs to this species has a blue body, wings only slightly fumose, with venation much like female; head hairy, elsewhere few and short hairs, none on femora, and fewer and shorter spines on tibia, inner spur three-fourths of basitarsus; there are few fine hairs on venter, no brush; the last two segments are peculiar, the upper margin of the penultimate is extended down as a high carina much above the convex surface of the ventrite, the next shows the short subgenital plate much elevated. Claws with tooth.

Length of fore wing 11 mm.

From same locality, 7 October (Plaumann). Type M.C.Z. no. 26237.

Pycnopompilus Ashmead

This is close to Psammochares but the tip of abdomen lacks the stiff bristles and has only a few fine hairs.

Table of species

1. Abdomen black, with a bluish and greenish sheen ..... *trochilinus*
   Abdomen rufous 2
2. First abdominal segment, as others, rufous ..... *dichromorphus*
   First segment of abdomen almost wholly black ..... *toltecus*

Pycnopompilus trochilinus Holmberg (Pompilus)

One female from San Juan, Argentine (C. S. Reed, Cornell Univ.). The clypeus is short, more than three times as broad as long, truncate below; vertex-width longer than second plus third antennal joints; ocelli in a broad triangle, laterals a trifle nearer to each other than to eyes; frontal groove distinct; no hair on basal antennal joint, short hair on front, longer on vertex; pronotum plainly angulate behind, with short hair above; propodeum moderately short, with hairs above, posterior slope with a broad, almost concave area; abdomen large at base, fine hairs at tip, longer ones on venter.

Legs not very strongly spinose, three, rather stout comb-spines on front basitarsus, last one not equal to second joint; mid and hind tibiae with rather short spines above, not one-half the diameter of joint; inner spur of hind tibiae nearly two-fifths of basitarsus; claws toothed. In fore wings the marginal cell nearly its length from wing-tip, as broad as second submarginal cell, latter one and one-half times as long below as broad, receiving first recurrent near tip; third submarginal little longer than second, narrowed more than one-half above, receiving second recurrent (curved) near middle; basal vein ends scarcely before transverse; in hind wings the anal vein ends just a little beyond forking of cubitus.

Pycnopompilus dichromorphus Rohwer (Psammochares)

Described from Cuzco, Peru; specimens from Rio Pativilca, Peru, 3,200 m., 20 May (Weyrauch); Oroya, Peru, 11 to 12,000 ft., 21 June (Parish, Cornell); Juniu Peru, 24 March (Amer. Mus. Nat. Hist.);

Psammochares escomeli Brethes, An. Soc. Cient. Argent. 93, p. 122, (1922) probably belongs to this genus; it is said to be green with reddish abdomen.

PYCNOPOMPILUS TOLTECUS spec. nov.

Very similar to *P. dichromorpha* Rohwer, but the basal segment of abdomen is almost wholly black, leaving only a very narrow border rufous; head and thorax showing more green than blue; femora and tibiae bluish; the fore wings brown, hind wings nearly hyaline. Hair on head and basal joint of antennae a little longer than in that species; the propodeum also with very long hair; at tip of abdomen only a few fine hairs.

Clypeus with lower margin plainly a little concave; second plus third antennal joints not nearly equal vertex-width; pronotum angulate behind; propodeum as in *dichromorpha,* with a median furrow. Legs have some hairs on femora; hind tibiae with two rows of rather short spines above, inner spur of hind tibia about one-half of basitarsus; venation about the same.

Length of fore wings 11 to 12 mm.

Females from Puno, Peru (S. Garman); also from Puno, Peru, 24 March (J. Soukup). Type M.C.Z. no. 26674, paratype A.M.N.H.

AUSTROCHARES gen. nov.

I use this for species similar to Psammochares in most points; the claws, however, in females are cleft, and the tip of abdomen lacks the stiff bristles, only very fine and usually short hairs.

Genotype is *Pompilus gastricus* Spinola.

The species known to me may be tabulated as follows:

1. Abdomen rufous 2
   Abdomen black 4
2. Front tarsi very short; third joint barely longer than broad; clypeus somewhat rufous; comb-spines rather short and stout 7
   Front tarsi of normal length; clypeus black 3
3. Comb-spines very long, sometimes broadened toward tip, four on basitarsus, longer than second tarsal joint ..... *gastricus*
   Comb-spines not so long, none broadened, and but three on basitarsus, hardly equal second tarsal joint ..... *satanus*
4. Four comb-spines on basitarsus; outer side of third submarginal cell curved 5
   But three comb-spines on basitarsus 6

5. Inner spur of hind tibia fully one-half of basitarsus; long hair on propodeum, pleura hairy, hairs on all femora above and below ..... *cujanus*
   Inner spur of hind tibia not one-half of basitarsus; less and shorter hair on propodeum, little if any on pleura, few hairs on front femora ..... *funebris*
6. Outer side of third submarginal cell nearly straight, cell not triangular; comb-spines on basitarsus small and far apart; first recurrent ends near apical third of second submarginal.... *elsinore*
   Outer side of third submarginal strongly curved, cell subtriangular; comb-spines of moderate length, each on basitarsus about reaching next; first recurrent ends near tip of second submarginal ..... *cordovensis*
7. Propodeum wholly silvery sericeous, pleura strongly so ..... *areatus*
   Propodeum and pleura scarcely if at all sericeous ..... *brevitarsus*

Pompilus fulgidifrons Fox probably belongs in this genus.

Austrochares gastricus Spinola (Pompilus)

This is a Chilean species, the comb-spines being excessively long and slender. Two females from San Ignacio, Argentine, 15, 23 March (Joergensen coll.) agree fairly well with the Chilean specimens, but the spines are not quite so long nor so slender. They have the third submarginal cell fairly broad above, not at all triangular, the marginal cell is elongate, little if any broader than the second submarginal; the male of the Chilean *gastricus* has the antennae black above and below. I have not seen an Argentine male. One female from San Juan, Argentine, 13 January (Joergensen) is larger, the third submarginal cell longer, the first recurrent ends at base of apical third of second submarginal; the comb-spines, four on basitarsus as usual, are not quite so long but thicker and the four on second and third joints are plainly spatulate; two females from Mendoza, Argentine, (C. S. Reed) (Cornell Univ.) have the comb-spines about as in the San Ignacio specimens, not quite typical.

Austrochares satanus Holmberg (Pompilus)

Holmberg based this on one male which had the antennae black above and somewhat rufous below; this, however, grades in a series of specimens to those with antennae rufous above and below, the latter Holmberg calls *gastricus* Klug. The abdomen in these males is much more depressed and broader than in the true *gastricus*. The

females which belong to these males are larger than *gastricus*, have but three comb-spines on basitarsus, all shorter, the third submarginal cell is triangular or nearly so, the marginal cell shorter and broader than in *gastricus*, the fore wing has a large area back of marginal cell and over third discordal which is nearly hyaline, and the dark of wing not near as dark as *gastricus*. Taschenberg's *gastricus* is evidently this species. It resembles somewhat the Chilean *diphonychus*, but the abdomen is broader in both sexes, and more depressed, the fifth ventral segment in male is broadly emarginate, while in *diphonychus* it is deeply emarginate in middle only.

Specimens are from Mendoza, 6, 12 December; La Paz, 20 December, both Argentine and both by Joergensen; Cosquin, Sierra de Cordoba, 1 to 9 March, also Argentine (Cornell Univ. Exped.).

Austrochares brevitarsus spec. nov.

Black; abdomen wholly rufous, clypeus rufous, hind margin of pronotum very narrowly pale whitish, spurs pale, wings yellowish fuscous, veins black; lower face silvery pubescent.

Clypeus truncate below, face little narrowed above; ocelli in broad triangle, laterals nearer to each other than to eyes; second plus third plus fourth antennal joint hardly longer than vertex-width; vertex, from in front, quite strongly convex. Pronotum broadly arcuate behind; propodeum short and high; front vertical, basal part very short, only about half the length of the steeply sloping posterior part; abdomen broad at base, moderately slender, tapering to the compressed last segment, which has a few hairs above and below.

Legs of moderate length, front tarsi very short, third joint as broad as long, fourth still shorter, comb of short but stout spines, three on basitarsus; hind tibia with two rows of spines above, four in each, widely separated, those of inner row the shorter, inner spur hardly one-half of basitarsus. In fore wings the marginal cell is about one and one-half its length from wing-tip, subtriangular, outer side straight and strongly oblique, broader than second submarginal cell, latter a little longer than broad, base curved, receiving the first recurrent vein near tip; third submarginal cell nearly as long below as second, above narrowed almost to a point, receiving the second recurrent (slightly curved) beyond middle; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 9.5 mm.

One female from Rio Yguagu, Paraguay, March (Donald Wees). Type M.C.Z. no. 26666.

In the sericeous hind margin of pronotum and band before scutellum it agrees with the description of *Pompilus areatus* Taschb. but the anal vein in hind wing scarcely goes beyond forking of cubitus.

Austrochares areatus Taschb. (Pompilus)

One female from Urucum, Corumba, Brazil, 23 to 29 December (Cornell Univ. Exped.).

Smaller than type, hardly 10 mm. long (type 14); it has the sericeous band on pronotum and in front of the scutellum, also silvery on all of propodeum, on pleura and coxae; the second, third, and fourth joints of front tarsi are short, but not broadened as in *brevitarsus*.

Austrochares elsinore spec. nov.

Female. Black, wings black-brown, hind wings paler, veins black, spurs black. Clypeus two and one-half times as broad as long, truncate below; face plainly narrowed, above, front with very short hair, longer on vertex, vertex-width about as long as the third antennal joint, ocelli in a low triangle, hind ones about as near to eyes as to each other; pronotum angulate behind, with short hair on front and shoulders; pleura bare; propodeum about as broad as long, low, from side the posterior slope nearly straight, with short hairs, mostly on sides, last segment above with few very minute hairs, last ventral segment with rather long hairs, most numerous near middle, other ventrites with few hairs. Three comb-spines on front basitarsus, not thickened, all equal to width of joint; mid and hind tibia with short spines above, rather thickly clustered on mid tibia, inner spur of hind tibia fully one-half basitarsus, inner point of claw sharp.

In fore wing with marginal cell a little more than its length from wing-tip, width not equal to that of second submarginal, latter longer below than broad, base curved, receiving the first recurrent near apical third; third submarginal fully as broad as long below, outer side nearly straight and oblique, top narrowed one-half, receiving the second recurrent (nearly straight) a little beyond middle; extension of medius about half-way to margin; basal vein interstitial with transverse; in hind wings the anal vein ends beyond forking of cubitus.

Length of fore wing 9 mm.

From Lima, Peru, 16, 21 May. Type, Cornell Univ., paratype M.C.Z. no. 26243.

Austrochares funebris Taschb. (Pompilus)

One female from Cordova, Argentina (Davis) agrees with description. Fox records it from Chapada, Brazil; described from Lagoa Santa, Mendoza, Tucuman, and Nova Friburg.

Fox, mistaking *funebris* for *funereus*, changed the name to *caliginosus*, but *funereus* Lepel. was described as an Anoplius, so even though it had been the same name, the change would be unnecessary.

Austrochares cordovensis spec. nov.

Female. Black, spurs black, wings black brown, vein black. Antennal third joint much shorter than vertex-width, ocelli in low triangle, hind ones nearer each other than to eyes, face but little narrowed above, very short hair on front, little longer on vertex; pronotum slightly angulate behind, hairs on shoulders very short, pleura with few hairs; propodeum very short, short, fine hair above, last abdominal segment with few fine hairs above, below more numerous, and also long ones on sides, few hairs on other segments.

Three rather long comb-spines on front basitarsus, those on following joints slightly curved, all a little thickened; mid and hind tibiae with stout and moderately long spines, inner spur of hind tibia about one-half of basitarsus; claws cleft; all femora with a few fine hairs above.

In fore wings the marginal cell is fully its length from wing-tip, width greater than that of second submarginal cell, tip oblique and straight; second submarginal longer than broad, little, if any, narrowed above, base curved, receiving the first recurrent near tip; third submarginal cell smaller than second, much narrowed above, outer side curved, receiving the second recurrent (slightly curved) at middle; extension of medius nearly as long as cell; basal vein interstitial with transverse; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 10 to 10.5 mm.

From Cordova (Davis), Mendoza, 6 December (Joergensen); Cosquin, Sierra de Cordoba, 1 to 9 March (Cornell Exped.), and La Rioja, August (Giacomelli), all in Argentine.

Type M.C.Z. no. 26233, paratypes there and at Cornell Univ.

The male is similar, but more slender; clypeus and lower face with whitish pubescence; vertex very broad as in female; lateral ocelli about as close to each other as to eyes.

Austrochares cujanus Holmb. (Pompilus)

Specimens from Mendoza, 6 December, 27 January (Joergensen); also La Rioja (Giacomelli); Chilecito, 29 February; Cosquin, Sierra de Cordoba, 1 to 9 March, all Argentine, and latter from Cornell Univ.

Episyron Schiodte

Episyron conterminus Smith (Pompilus)

From Lima, Peru (Soukup coll.) and Santa Cruz, Bolivia, (Steinbach). Fox records it from Chapada and Pedru Branco, Brazil; also one from Campinas, Brazil, March (Williams). *Pompilus mesothoracicus* Brèthes may be the same species.

The marginal cell is more than its length from wing-tip, stigma short, obliquely truncate at tip, abscissa three about one-half of abcissa two, fourth abcissa longer than third plus second, second recurrent ends at outer third, first recurrent at outer third also, the comb of long and slender spines, some slightly curved, four on the basitarsus.

Episyron fraternus spec. nov.

Female. Body black, legs black, hind femora and tibiae rufous, spurs brown, antennae black; wings hyaline, dark apical spot reaching only tip of marginal cell, veins and stigma black. Face with a narrow white line on each orbit, and a finer one behind each eye; pronotum with a greenish white hind border, no pale band on abdomen; lower face and clypeus densely white pubescent, silvery on collar, no curved band across pronotum; propodeum not as strongly silvery as in *E. conterminus*; face with longer white hair than in *conterminus*.

Structure very similar to *conterminus*; the hind ocelli as near eyes as to each other; comb of fine long spines; second plus third antennal joints equal vertex-width; inner spur of hind tibiae nearly four-fifths of basitarsus; hind tibiae with reddish bristles.

Venation much as in *conterminus*; marginal cell fully its length

from wing-tip, about as broad as second submarginal cell, latter one and one-half times as long below as broad, not one-half as long above, base straight, sloping, receiving first recurrent before apical third; third submarginal cell shorter below than second, narrowed more than one-half above, receiving the second recurrent (nearly straight) beyond middle, this cell more than twice its length from outer margin of wing (in *conterminus* not so far).

Length of fore wings 7 mm.

One female from Lima, Peru (Soukup coll.). Type M.C.Z. no. 26774.

Readily separated from *conterminus* by white (instead of yellow) markings, and absence of the band on abdomen, the dark spurs, and no curved band of white scales across front of pronotum.

Aporinellus Banks

This genus has the propodeum projecting each side behind in an almost pointed process; second and third submarginal cells united, and receiving both recurrent veins; stigma very short; claws cleft; fore wings with a folding-line.

Aporinellus apicipennis Brèthes (Aporus)

Two from Santa Cruz, Bolivia (Steinbach), and two from Piracicaba, Brazil, February (Williams). The male agrees with the female in having a silvery band across tip of four segments; head and thorax generally silvery; leaving a black band on pronotum before tip, some of mesonotum, most of scutellum, and base of propodeum black. The second plus third submarginal cell has each end oblique, the second recurrent vein ends a little before tip; the first recurrent ends about one-fifth way out; inner spur of hind tibia about two-thirds of basitarsus, and outer spur but little shorter.

Sophropompilus Ashmead

By the very short antennal joints the following species will go to Sophropompilus but the segments of abdomen are much constricted at base, quite different from the genotype.

Table of species

1. Head densely clothed with long black hair; tips of wings darker ..... *peruanus*
   Head only sparsely hairy 2
2. Fore wings not very dark, the area beyond cells much darker.. *coeruleus*
   Fore wings nearly evenly dark, almost black ..... *copiosus*

SOPHROPOMPILUS PERUANUS spec. nov.

Female. Bright blue, antennae and tarsi black, fore wings blue on base, membrane lightly suffused but the area beyond cells much darker as in *coeruleus*; hind wings dark only near tip; thorax in some views metallic green. Head, thorax, coxae and femora much more hairy and hairs longer than in other species; clypeus hairy all over, front with some hairs about as long as first antennal joint; base of abdomen above with short hairs and below more hairy than usual; all femora with long scattered hairs.

Clypeus about three times as broad as long, lower margin scarcely arcuate; antennae very short, much as in other species, third joint hardly twice as long as second; face not narrowed above, front with the usual deep groove, ocelli in low triangle, hind ones about as near eyes as to each other; pronotum broadly arcuate behind, propodeum short, posterior slope rather flattened, quite densely haired; abdomen with second, third, and fourth segments appearing somewhat constricted at base, a few very fine short hairs at tip, below with moderately long hairs on all segments. Legs short, front basitarsus with three comb-spines, each fully reaching to next; hind tibia with inner spur reaching fully to middle of basitarsus.

Fore wings with marginal cell much more than its length from wing-tip; about as wide as submarginal cells, outer end straight and oblique; second submarginal cell a little longer than high, both ends somewhat outcurved, receiving the first recurrent vein about one-fourth before tip; third submarginal cell about as long below as second, much narrowed above, outer side curved, receiving the second recurrent (slightly curved) near middle; extension of medius as long as third cell; basal vein interstitial with transverse; in hind wings anal vein ends a little beyond forking of cubitus.

Length of fore wing 9 mm.

From Victoria, Dept. Juin, Peru, July 1939 (W. F. Walsh); Juniu, Peru, 24 March (Amer. Mus. Nat. Hist.). A male from Trujillo, Peru, November 1939 (Weyrauch coll.) is more purple on propodeum

and abdomen above, it has the dense long hair on head and over all of clypeus, also on thorax and propodeum, but none on femora, more hair and longer on base of abdomen, latter somewhat flattened; the second submarginal cell a little longer than in female, both ends straight, the third submarginal much shorter and nearly triangular; the inner spur of hind tibia a little longer than in female.

Length of fore wing 7 mm.

Type M.C.Z. no. 26239; paratype A.M.N.H.

Sophropompilus copiosus spec. nov.

Female. Body deep blue to purplish, femora more or less purple; wings black-brown, veins black; spurs pale brown. Clypeus about two and one-half times as broad as long, below nearly straight, no bristles on surface; face broader than high, scarcely narrowed above; anterior ocellus in a deep pit, and a line from it to antennae; lateral ocelli nearer each other than to eyes; face bare except for a few short hairs on vertex, vertex-width nearly as long as second plus third plus fourth joints of antennae; pronotum rather long arcuate behind, only extremely minute hairs; mesopleura with a few moderately long hairs; propodeum short, very high, posterior slope long and broadly slightly concave, the lateral margins almost forming a ridge, with few long hairs above and on posterior sides.

Abdomen high, a few hairs on basal part of first segment above; tip practically bare, under side of last segment with a few hairs on all segments. Legs short; three comb-spines on front basitarsus, thickened, the first and second reaching the next; a few long hairs on front and mid femora, mostly above; inner spur of hind tibia more than one-half of basitarsus, claws with a small tooth.

In fore wing marginal cell more than length from wing-tip, outer side straight, as broad as the submarginal cells; second submarginal nearly one and one-half times as long as broad, base curved and sloping a little, receiving the first recurrent at last fourth, third shorter below than second, outer side curved and sloping to make cell almost triangular, receiving the second recurrent (slightly curved) at middle; extension of medius much longer than cell; basal vein interstitial with transverse; in hind wings the anal ends a trifle before cubital fork.

Length of fore wing 9 mm.

From Cosquin, Sierra de Cordoba, 1 to 9 March (Harris). Type at Cornell Univ., paratype at M.C.Z. no. 26245.

Sophropompilus coeruleus Taschenb. (Pompilus)

From Santa Cruz, Bolivia (Steinbach); and La Rioja, Argentina (Giacomelli, Cornell).

Aridestus gen. nov.

This genus is similar to the North American Ridestus in having the propodeum striate transversely. The propodeum is very different in shape, it is swollen laterally, and the posterior slope is largely concave. Antennae short, but the joints not so short as in Sophropompilus; the comb is composed of long slightly curved spines; claws with a small tooth. Body with few hairs, front coxae with no long hairs, only a few very short and pale, practically invisible.

The marginal cell is short, triangular, and almost twice its length from tip of wing; the stigma is fully as long as abscissa one; the legs are slender and the mid and hind tibiae have spines above of moderate size.

Aridestus bergi Brèthes (Pompilus)

A female from Villa Rica, Paraguay (Schade). Face broad; vertex broader than third plus fourth joints of antennae; ocelli in broad triangle, hind ones almost as near eyes as to each other; pronotum rounded in front, arcuate behind; median groove of propodeum distinct on base; tip of abdomen with a few fine hairs; legs slender, inner spur of hind tibia about two-thirds of basitarsus; both second and third submarginal cells small and nearly triangular, the second rather the larger.

Sericopompilus Ashmead

The species have three rows of spines above on hind tibiae, a row of larger spines each side and an intermediate row of smaller spines. There is little hair on the body, but nearly all species are sericeous; the clypeus is very broad; in males often partly white; and there may be differences in color marks in the males. The scutellum is compressed and elevated; the stigma very large.

1. Pronotum rufous; fore wings with two dark bands; basal joint of antennae pale ..... *accoleus*
   Pronotum black 2

2. Legs mostly black 3
   Legs (except coxae and trochanters) pale yellowish ..... *minutus*
3. Base of second segment pale yellowish, base of tibia also yellowish ..... *lucanus*
   Legs wholly black; abdomen with a large whitish spot each side on second and third segments ..... *exilis*

Sericopompilus accoleus spec. nov.

Female. Head black, clypeus and mandibles (except tip) yellowish; antennae brown, first and second joints yellow; pronotum dull rufous, lower part of side lobes nearly hyaline; mesonotum also dull yellowish; scutellum, rest of thorax, propodeum, and abdomen shining black; much of body with a fine whitish pile, dense and silvery on lower part of face, and a band across tip of propodeum; legs mostly black, but front tibiae and tarsi mostly yellowish, hind tibia with a white basal band above, mid and hind spurs white; wings hyaline, a broad dark band over basal and transverse veins, and a broader one over marginal, second and third submarginal cells and extending into upper outer part of the third discoidal cell, tip of wings scarcely darker, stigma black, veins brown.

Clypeus fully three and one-half times as broad as long, lower margin barely rounded; face slightly widened above, and then narrowed on vertex; antennae rather short, but second plus third joints nearly equal vertex-width; ocelli in a very low triangle, the laterals much smaller than anterior ocellus and plainly nearer to eyes than to each other; a few very fine short hairs on vertex, otherwise body bare.

Scutellum compressed and elevated; propodeum as broad as long, evenly sloping, suture in mesopleura very indistinct; abdomen with basal segment about as long as broad behind, rather broad at base; legs very smooth, front tibia with a few spines at tip, and two extremely minute ones on lower outer side; mid and hind tibia above with moderately long but slender spines, many about as long as width of joint; on hind tibia above a median row of very short spines between the two main rows, inner spur of hind tibia three-fourths of basitarsus, last tarsal joint of all legs smooth beneath; claws almost bifid, the tooth being long, slender, slightly oblique, and much beyond middle of claw.

In fore wings the marginal cell is nearly its length from wing-tip, and as broad as second submarginal cell, the latter hardly one and

one-fourth times as long below as broad, base curved, and slightly oblique, outer side scarcely oblique, receiving the first recurrent vein at apical fourth; third submarginal cell a little longer below and a little shorter above than the second, widened toward tip, receiving the second recurrent (but little curved) near middle, median extension fully one-half way to outer margin; basal vein ending a little before transverse; in hind wings the anal vein ends a little before forking of cubitus.

Length of fore wing 8.5.

One female from Maracajú, Matto Grosso, Brazil, April-May (Fairchild). Type M.C.Z. no. 26598.

The male is similar in color and general structure. The rufous of thorax extends over most of mesopleura, and over scutellum and metanotum; the clypeus is black as also the basal joint of the antennae, but the third joint if pale on apical half; the bands on wings are not as broad, particularly the one over the basal vein.

The thorax and propodeum are very broad as in the female, but the abdomen is hardly one-half the width, somewhat compressed, and with a white spot at the tip. The scutellum is fully as elevated and compressed as in the female; the pubescence on propodeum is mostly behind and so parted as to leave the bare anterior part in a V. The spines on mid and hind tibiae are scarcely shorter than in female, the mid row distinct; the venation is the same.

Length of fore wings 6 mm.

One from Campinas, Sao Paulo, Brazil (F. X. Williams).

Sericopompilus lucanus spec. nov.

Female. Body and legs black, shining, especially on the propodeum and abdomen. Clypeus mostly rufous, but the upper edge is black; mandibles (except tips) yellowish; antennae brown, but basal joint yellowish, and second and third joints yellowish below; no marks on thorax, propodeum, nor abdomen; front tibia and tarsus yellowish, mid and hind tarsi brownish, a white spot above near base of hind tibia, mid and hind spurs white. Wings hyaline, stigma and veins dark brown, two brown bands similar to those of *S. accoleus*, but the first is over only the lower section of basal vein, and is slightly paler than the outer band, wing-tip scarcely darkened. Structure practically identical with *S. accoleus* except that the tooth on claws is small, erect, and near middle of claw; the marginal cell is a trifle nearer wing-tip, and the second recurrent veins ends plainly beyond

the middle of third submarginal cell; in hind wings the anal vein ends further before the forking of cubitus; the legs have the same length and spination as in *S. accoleus*, the inner spur of hind tibia is shorter, fully two-thirds of basitarsus; the lateral ocelli are a little nearer to eyes than in the allied species.

Length of fore wing 7 mm.

One female from Nova Teutonia, Santa Catharina, Brazil, 25 January (F. Plaumann). Type M.C.Z. no. 26597.

A male taken at same place one day later is doubtless the male of this species; the wings agree very well, the second submarginal cell being much longer than broad. The clypeus is black in middle, the sides obliquely white; the pronotum white on hind border; the second segment of abdomen has a white band at base, the tip white. The abdomen is very slender. The spines on hind tibia above are much smaller than in the female, the inner spur about four-fifths of the basitarsus; the front tibiae white at base and tip, front tarsi also pale; mid and hind tibiae with a white mark at base forming a ring around the joint.

Length of fore wings 5.5 mm.

Sericopompilus exilis Banks.

Described from British Guiana and Surinam, only males known.

Sericopompilus minutus spec. nov.

Body black; legs pale yellowish, but the coxae and trochanters black; wings nearly hyaline, a pale brown cloud over marginal and second and third submarginal cells. Clypeus mostly pale rufous, mandibles wholly pale rufous; antennae yellowish on basal joint, beyond brown, darker above toward tip; hind margin of pronotum dull yellowish; hind tibiae with a white spot at base, but scarcely paler than the yellowish around it, spurs white. Much of body with a fine whitish pubescence most evident on lower face, pronotum, sides of propodeum, and the coxae beneath.

Clypeus very broad, the raised lower margin truncate; face broad, somewhat narrowed above, ocelli in a large triangle, laterals about as near eyes as to each other, anterior ocellus in a pit; antennae short, second plus third plus fourth joints about equal vertex-width. Pronotum lightly arcuate behind, from side much sloping in front and slightly rounded; propodeum short, from side evenly curved, no hairs

above; abdomen rather short, fairly broad near base, shining above, a few hairs on last segment above, and some quite long ones below and elsewhere on venter. Legs not long, with distinct spines, hind tibia with three on each side above and between is a row of about six shorter spines; inner spur nearly three-fourths of basitarsus; claws stout, with a very small tooth.

In fore wings the marginal cell is about its length from wing-tip, last abcissa of radius straight and sloping, more than one-half costal length of cell, in width about equal to second submarginal cell, latter longer below than broad, base curved and narrowing top about one-fourth, receiving the first recurrent vein near middle; third submarginal not quite so long below and only one-half as long above as the second, outer side lightly curved, receiving the second recurrent vein (nearly straight) at middle; in hind wings the anal vein ends much before the forking of cubitus.

Length of fore wings 5 mm.

One female from Tres Lagoas, Matto Grosso, Brazil, 6 to 10 December (Cornell Univ. Exped.).

Allocyphonyx Ashmead

The presence of a distinct malar space has been considered an essential character of this genus. In the South American forms some have it as long as in our North American forms, but others have the eyes almost reaching the lower margin of the head, only a very narrow space between. The exposed labrum, together with the cleft claws, is sufficient to distinguish the females, but the shape of the last abdominal segment, sloping upward on under side, and the small triangular third submarginal cell and the small marginal cell, remote from wing-tip, are helpful.

In the male the antennae, thick, not very long, and at least some of the joints swollen near middle or near one end are characteristic, as also the dense, erect white hair at the tip of the propodeum.

Viewed from the side the head is hung low down, and the pronotum and mesonotum are evenly arched above it.

The species with almost no malar space agree with the African genus Atopopompilus, and I shall consider it a subgenus of Allocyphonyx.

Table of females

1. Abdomen rufous; pronotum with a yellow hind border; malar space about one-half as long as broad 2
   Abdomen black; pronotum not pale behind; malar space very short, eye nearly reaches to margin — subgenus Atopopompilus 3

2. Head, thorax, propodeum, and coxae strongly sericeous; tarsi pale, black at ends of joints ..... *semiplumbeus*
   Thorax, propodeum, and coxae not or scarcely sericeous, tarsi wholly dark ..... *diabolicus*

3. Marginal cell twice its length from wing-tip; body not over ten millimeters long; a small pit at base of propodeum ..... *minor*
   Marginal cell not twice its length from wing-tip; body more than ten millimeters long 4

4. Pronotum, from side, in even curve, scarcely any top in middle. *fairchildi*
   Pronotum, from side, not in even curve, the top long and flattened 5

5. Last three segments of abdomen cinereous ..... *sulcatus?*
   Last three segments not cinereous 6

6. No hyaline spot in first discoidal cell of fore wing ..... *neriene*
   A hyaline spot in first discoidal cell ..... *alienus*

Table of males

1. Abdomen rufous, last segment white above, head and thorax black, pronotum bordered behind with yellowish; tarsi pale, black at tips of joints ..... *semiplumbeus*
   Abdomen black, several segments partly or wholly with blue-gray bands 2

2. Pronotum bordered behind with yellowish 3
   Pronotum wholly dark, at most somewhat sericeous 4

3. Basal bands on first, second, and third segments, fourth wholly sericeous ..... *amoenissimus*
   Basal bands on first and second segments, third and fourth wholly sericeous, fifth segment black ..... *scapulatus*

4. Basal bands on all of first four segments, none wholly sericeous; antennae very strongly crenulate along middle part ..... *serraticornis*
   Basal bands on two or three segments, at least one wholly sericeous 5

5. Fourth segment wholly sericeous, one, two, and three with basal band, fifth black ..... *sericeus*

Both third and fourth segments wholly sericeous, fifth black; pronotum faintly bordered behind with bluish gray.....*incalis*
Fourth, fifth, and sixth segments sericeous, first, second, and third with basal band.....*affinis*

Allocyphonyx semiplumbeus Taschb. (Pompilus)

The *Pompilus annulipes* Fox is the male, and perhaps *Pompilus iratus* Smith is also the same.

Described from Parana, I have both sexes from Campinas, Sao Paulo, Brazil, February and March (F. X. Williams); also males from La Rioja, Argentine.

The head, thorax, propodeum strongly sericeous. The malar space of female is about as long as in our northern *A. maura*; ocelli in broad triangle and hind ones about as near eyes as to each other; antennae slender, second plus third joints about equal vertex-width. The third submarginal cell is not quite triangular; inner spur of hind tibia one-half of basitarsus. The male is similar, but smaller, and the pale parts of hind tarsi usually more pale than in female. The joints along middle of male antennae are not as much modified as in the other species.

Allocyphonyx diabolicus Holmb. (Pompilus)

Several females from Villarica, Paraguay, January (Schade coll.) (Cornell); Urucum, Corumba, Brazil, 23 to 29 December (Cornell Univ. Exped.) and Cosquin, Sierra de Cordoba, Argentina, 1 to 9 March (Cornell Univ. Exped.).

The insect has very little hair anywhere; the clypeus is subtriangular, truncate below; second plus third joints of antennae not equal vertex-width; lateral ocelli about as near each other as to eyes; pronotum angulate behind; propodeum with median groove; last segment of abdomen compressed; mid and hind tibiae with a few stout spines above, inner spur of hind tibia almost one-half of basitarsus.

In fore wings the marginal cell short, more than its length from wing-tip, fully as broad as second submarginal cell, latter longer below than broad, receiving first recurrent a little before tip; third submarginal sometimes a little shorter than second, nearly triangular, outer side curved, receiving the second recurrent vein (curved) before middle; basal vein interstitial or nearly so with the transverse; in hind wings anal at or just before forking of cubitus.

ALLOCYPHONYX SERRATICORNIS Taschenberg (POMPILUS)

Male from Campinas, Sao Paulo, Brazil, February (F. X. Williams).

Face, clypeus, pronotum largely sericeous, under side of basal antennal joint yellow; bluish white band across base of first four segments above, fifth wholly black, sixth and seventh more white at tip.

Joints five to ten of antennae very strongly modified, quite suddenly swollen at base; inner spur of hind tibia fully four-fifths of basitarsus, that of mid tibia almost equal basitarsus.

Marginal cell about one and one-half its length from wing-tip, broader than second submarginal cell, latter as long as outer side of marginal cell, base slightly curved, first recurrent vein ends beyond middle; third submarginal cell not quite pedicellate, each end curved a little, the second recurrent vein ends beyond middle.

ALLOCYPHONYX SERICEUS spec. nov.

Black, hind tibiae white above on basal half, spurs white; last segment of abdomen white above; wings nearly hyaline, pale brown beyond cells; postscutellum nearly white; antennae brown or rufous on basal half, basal joint pale beneath. Head, thorax, coxae and femora almost entirely covered with white pubescence, not so prominent on upper face, vertex, mesonotum, and scutellum. Abdomen with bluish grey band across base of first, second and third segments, fourth almost wholly blue-gray. Fine, erect, white hair on face and vertex, and some below on basal joint of antennae.

Clypeus truncate below; antennae short, joints six to twelve modified as usual, second plus third plus fourth joints hardly more than vertex width; lateral ocelli much nearer each other than to eyes; pronotum rather shallowly angulate behind; propodeum short, apical part densely covered with snow-white hair; abdomen slender, fully as long as head and thorax; legs quite short, spines on mid and hind tibiae fairly long, inner spur of hind tibiae two-thirds of basitarsus.

In fore wings the marginal cell is broadly triangular, about twice its length from wing-tip, at end of second submarginal cell it is broader than that cell; latter nearly square, receiving the first recurrent at apical third; third submarginal triangular and petiolate, shorter than second, receiving the second recurrent near middle, and end of cell is over four times its length from wing-margin; basal vein ends a little before transverse; in hind wings anal vein ends at forking of cubitus.

Length of fore wings 5.8 mm.

Two males, type from "Juis de Fora," Brazil, Thayer Exped., other from Vista Alegre, Rio Branco, Amazonas, Brazil, 6 September (Bequaert). Type M.C.Z. no. 26668.

Allocyphonyx scapulatus Brèthes (Pompilus)

Specimens from Mendoza, Argentine, 8 January (type locality and same collector, Joergensen) and also from Santa Cruz, Bolivia (Steinbach); other from Mendoza (C. S. Reed) Cornell Univ.; Buenavista near Santa Cruz, Bolivia (Steinbach, Cornell) and Passo Fundo, Rio Grande do Sul, Brazil, 8 January (Cornell Univ. Exped.). Scapulatus differs from the description of *Pompilus amoenus* Taschenberg only in having mid and hind tarsi wholly dark instead of pale with black tips to joints; it may be but a variety. The second plus third plus fourth antennal joints hardly equal vertex width; marginal cell about twice its length from wing-tip, third submarginal triangular or barely petiolate, much shorter below than second, receiving the second recurrent beyond middle, tip of third cell nearly four times its length from margin of wing; inner spur of hind tibia fully two-thirds of basitarsus.

Allocyphonyx incalis spec. nov.

Black, last segment of abdomen white above; spurs brownish; wings brown, a pale area behind marginal cell, beyond the cells is a broad dark brown band; hind wings paler brown, darker at tip. Clypeus with white pubescence, face with grayish pubescence; pronotum with blue-gray pubescence, most strong on hind part, a similar patch each side of scutellum; posterior slope of propodeum with dense white hair with a bluish sheen beneath; blue-gray bands across base of first and second segments of abdomen, third and fourth wholly blue-gray, beyond less distinct; mid and hind tibiae and basitarsi also bluish above, coxae and pleura not silvery. Clypeus, face, back of head, and first joint of antennae with much short black hair, also shorter on pronotum; a few short hairs on venter.

Clypeus truncate below; antennae with joints six to twelve, strongly swollen near base in usual manner in the genus; lateral ocelli much closer to each other than to eyes; pronotum deeply angulate behind; propodeum slightly narrowed toward abdomen; latter slender, about as long as head plus thorax; legs moderately slender, hind tibiae with

a few spines above, some as long as diameter of the joint, tarsi with long spines at tip of joints, inner spur of hind tibia about two-thirds of basitarsus.

In the fore wing the marginal cell is nearly triangular, and almost twice its length from wing-tip, at tip of second submarginal cell it is as wide as that cell, latter fully one and one-half times as long below as broad, vein at base slightly curved above, receiving the first recurrent vein near tip; third submarginal cell triangular or almost so, much shorter than second, outer side curved, receiving the second recurrent (nearly straight) beyond middle, tip of third cell about three times its length from wing-margin; basal vein ends a little before transverse; in hind wings the anal vein ends a little beyond forking of cubitus.

Length of fore wing 9 mm.

One male from Ninabamba, near Ayacudo, Peru, 1900 m., December (Weyrauch).

Type M.C.Z. no. 26669.

A male, very similar and probably same species has the coxae and pleura more silvery, the spurs nearly white, little hair on clypeus or basal antennal joint; abdomen more fully covered with bluish gray pubescence, no white spot on last segment, venation same except in hind wing the anal is interstitial.

From la Sombra, Putumayo District, Peru, 22 August (Cornell Univ. Exped.).

Allocyphonyx affinis spec. nov.

Black; face, clypeus, pronotum, front coxae in front, white pubescent, but hardly silvery, nearly so on clypeus; antennae pale yellow on under side of first joint, third, fourth and fifth joints rufous below; hind tibiae with white stripe near base above, spurs brownish; fore wings dark, but hyaline spot in first discoidal cell, tip darker than in *serraticornis*.

In general agrees with *serraticornis*, antennae very similar, but the abdomen has a bluish white band across base of first, second, and third segments, fourth, fifth, and sixth wholly bluish white. Marginal cell a little more than one and one-half its length from wing-tip, outer side longer than first plus second abcissae, not broader than second submarginal cell, latter almost as broad as long below, narrowed a little above, receiving first recurrent about one-fourth from tip, third submarginal pedicellate, second recurrent vein (curved) ends just

beyond middle. In general structure about like *serraticornis*, but abdomen has the bluish white bands across base of first, second, and third segments, the others beyond wholly bluish white.

Length of fore wings 8 mm.

A male from Mera, Ecuador, February (F. X. Williams). Type M.C Z. no. 27135.

Subgenus Atopopompilus Arnold

The species described below agree well with specimens of *Atopopompilus mlanjiensis* and *A. marshalli*, I have not seen the type species. But I consider them only a subgenus of Allocyphonyx; they differ in having a very short malar space, but they have the exposed labrum, cleft claws and other characters of Allocyphonyx. The length of the malar space varies in species of Allocyphonyx, and the males have it shorter; some of the males described in Allocyphonyx are probably males of the species below.

A. (Atopopompilus) neriene spec. nov.

Female. Black, clypeus and lower face more or less silvery, fore wings blackish, third discoidal and area behind paler, hind wings pale behind cubital fork and behind anal vein, spurs brown. Face narrow, about as broad on vertex as below, clypeus a little more than twice as broad as long, vertex-width longer than third joint of antennae, latter scarcely longer than fourth; hind ocelli nearer eyes than to each other; moderately short hair over vertex and front. Pronotum angulate behind, dorsal part rather long before bending down, some short scattered hairs; pleura bare; propodeum very low, at first nearly flat but grading evenly into the short posterior slope, an apparent median groove, the spiracles oblique, large, and nearly length from front margin; basal segment of abdomen rather long, apex above with a few fine hairs; last ventral segment with some fine hairs below and on sides, little on other segments. Legs slender, front basitarsus with but two very short spines on outer side, second joint nearly twice as long as third; hind tibia with some long spines fully the diameter of the joint, inner spur of hind tibia from fully half to nearly two-thirds of basitarsus; claws cleft.

In fore wings the marginal cell is very short, about one and one-half its length before wing-tip, as broad as second submarginal cell, the latter longer than broad, little narrowed above, receiving the

first recurrent vein at apical third; third submarginal triangular, sometimes pedicellate, shorter below than second, outer side curved and sloping, receiving the second recurrent (scarcely curved) near middle; extension of medius not reaching half way to margin; basal vein a trifle before transverse or interstitial; in hind wings the anal vein ends at forking of cubitus.

Length of fore wing 11 mm.

From Cosquin, Sierra de Cordoba, Argentine, 1 to 9 March (Harris), and Mendoza, Argentine (Reed). Type at Cornell Univ., paratype M.C.Z. no. 26244.

A. (Atopopompilus) neriene var. alienus var. nov.

Very similar to typical form; face and clypeus silvery. Face narrower below so clypeus is more triangular; third antennal joint only a little longer than fourth; inner spur of hind tibia a little over one-half of basitarsus; wings dark, paler in first submedian and second discoidal cell, second submedian cell hyaline white; venation very similar. Size the same.

From San Ignacio, Argentine, 15 March (Joergensen). Type M.C.Z. no. 26238.

A. (Atopopompilus) minor spec. nov.

Body black, abdomen rather more brown toward tip, clypeus and sides of lower face silvery and a small, less silvery, spot at each posterior corner of the propodeum; legs and antennae black; wings dark brown, veins and stigma black. Some erect fine hairs on front and vertex, some on last segment of abdomen above and below, a few very fine ones on front coxae.

Clypeus hardly three times as broad as long, slightly, evenly concave on lower margin; eyes not quite reaching mandibles; face only a little narrowed above, ocelli in a broad triangle, hind ocelli nearer to eyes than to each other; second plus third antennal joints much shorter than vertex-width, the third joint but little longer than fourth.

Pronotum rounded and sloping in front, arcuate behind; propodeum about as broad at base as long, with a rather large pit in middle of base, from side, evenly rounded; mid and hind tibiae and their basitarsi with a few fairly long spines, inner spur of hind tibia more than one-half of basitarsus.

In fore wings the closed cells are further from tip of wing than

usual, the triangular marginal cell fully twice its length from wing-tip, as broad as second submarginal cell, latter but little shorter below than marginal cell on costa, the top fully one-half as long, base curved, receiving first recurrent vein one-fourth from tip of cell; third submarginal very small, quite long pedicellate, below hardly one-half of second, the second recurrent ends a trifle beyond middle.

Length of fore wing 6 mm.

One female from Campinas, Sao Paulo, Brazil, February (F. X. Williams). Type M.C.Z. no. 27134.

A. (Atopopompilus) sulcatus Fox

A female from Campinas, Brazil, March, agrees quite well with the description of this species.

A. (Atopopompilus) fairchildi spec. nov.

Deep black on body, legs, and antennae, wings pale brown, darker beyond cells; few fine hairs on clypeus, face, and vertex, shorter on pronotum, long fine hairs at tip of abdomen, few and short on venter.

Clypeus subtriangular, truncate below, the short sides oblique, upper edge almost angled in middle; face little narrowed above, a fine median line; lateral ocelli nearer to eyes than to each other; second plus third antennal joints about equal vertex-width; pronotum angulate behind; evenly and lightly curved as it slopes to collar, hardly any above in middle; propodeum as long as broad, sides parallel, no median groove except near base, posterior part short compared with basal part, from side evenly sloping to the turn.

Abdomen with basal segment fully as long as broad at tip; second segment not wider, sides parallel; legs moderately short, but mid and hind tarsi long, very spiny, some spines above longer than width of joint; inner spur of hind tibia more than one-half of basitarsus, and basitarsus with spines much longer than width.

In fore wings the marginal cell fully one and one-half times its length from wing-tip, subtriangular, outer side straight, strongly oblique; at end of second cell the marginal cell is as wide as that cell, latter about one and one-half times as long below as broad, base curved, receiving the first recurrent near apical third; third submarginal cell small, little more than one-half as long below as second, petiolate above, outer side curved, receiving the second recurrent close to

middle, its tip more than three times its length from wing-margin; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 10 mm.

One female from Maracajcú, Matto Grosso, Brazil, April-May (Fairchild). Type M.C.Z. no. 26667.

(Atopopompilus) amoenissimus D. T.

This is the *Pompilus amoenus* Taschenberg, but the name being preoccupied, was changed by Dalla Torre. A male from Campinas, Sao Paulo, Brazil, March (Williams).

Psorthaspis Banks

Psorthaspis bequaerti Bradley

From Partidas, Cincinnati, San Lorenzo Mt., Colombia.

Aulocostethus Haupt.

Aulocostethus excelsus Bradley

From Nova Teutonia, Santa Catharina, Brazil, 22 January, (Plaumann).

Aulocostethus haupti Arlé

A female from Campinas, Brazil, March, agrees well with the original description. In general similar to *A. excelsus* but the propodeum and coxae black, a white mark on sides of propodeum and a white streak on mid and hind coxae.

Epicostethus gen. nov.

This has the venation as in Aulocostethus, the second submarginal cell oblique and bent down in middle of lower margin. It differs at once in the much shorter pronotum, angulate behind, in middle not one-third as long as in Aulocostethus; the front femora while somewhat thickened, are not nearly as much so as in Aulocostethus; the antennae are fully as slender, but the joints are not much narrowed

toward base; the stigma and anal vein as in Aulocostethus; it is an offshoot of that genus and not closely related to the Australian *Epipompilus*.

Genotype EPICOSTETHUS WILLIAMSI spec. nov.

Female. Body black, propodeum and abdomen shining; legs brown, femora quite dark, somewhat reddish beneath, spurs pale brown; antennae brown; a small pale yellowish spot on each side of the second abdominal segment, and another near base on hind tibia, also the first and base of third antennal joints whitish, most distinct below; clypeus with a rufous margin; clypeus, basal half of antennae, apical half of abdomen with much fine pale yellowish to whitish hair or pubescence, elsewhere covered with short erect hair, longer on posterior slope of propodeum, and some much longer on vertex; legs mostly covered with a very fine pubescence.

Fore wings with a brown band over basal and transverse veins, much wider behind, a broad band covering the marginal cell and as wide behind, and more apical half of third discoidal.

Head much as in Aulocostethus; maxillary palpi long, dark; clypeus short, truncate below; the frontal groove distinct only below; ocelli in a low triangle, hind ones nearer eyes than to each other; eyes very hairy; from in front the vertex is slightly convex, its width about equal to the second plus third plus fourth antennal joints.

Pronotum not one-half as long as mesonotum, behind broadly and quite deeply arcuate, almost angulate in middle; propodeum from side nearly flat for two-thirds its length, then the gentle posterior slope; abdomen about as broad as mesonotum. Legs short; front and mid femora slightly swollen (not as much as in Aulocostethus), mid and hind tibiae have minute short spines above, not rising above the hair-covering; inner spur of hind tibiae equal one-half of basitarsus.

Venation in general much as figure 11 of Plate XI of Kohl, 1886, but marginal cell broader, basal vein interstitial with transverse vein, and second and third submarginals more like Aulocostethus.

Length of fore wings 6 mm.

One female from Banos, Oriente, Ecuador, 6,000 ft., 30 October (F. X. Williams). Type 26777.

It is not an Aulocostethus, I presume that the type of Epipompilus has a long pronotum, so this species can hardly go there, but it is related to *Epipompilus delicatus* Turner from Panama which is said to have a short pronotum; it is very different from the New Zealand species described in Epipompilus.

Notoplaniceps Bradley

Notoplaniceps fenestralis Bradley

From Muzo, Dept. Boyaca, Colombia 900 m.; Vista Nieve, San Lorenzo Mt., Colombia, 18 December (both Bequaert), and Mazaro Bay, Trinidad, 29 November (N. A. Weber).

Aporus Costa

Aporus canescens Smith

A female from Vista Nieve, San Lorenzo Mts., Colombia, 16 December (Bequaert), has the sericeous bands at base of the abdominal segments, and the wings have the coppery iridescence mentioned by Smith.

Body with only a few fine hairs;

The head and pronotum are much less densely haired than in *Notoplaniceps fenéstralis*, and no hyaline spots in the fore wings; the second recurrent ends at the end of second plus third submarginal cell.

Two males taken at same place, December 18, are doubtless this species, the second plus third cell is shorter than in the Trinidad male of *fenestralis*.

Euplaniceps Haupt

This genus belongs with the series in which the head is flattened and the antennae are situate at the clypeal margin. The front femora are more or less swollen, the abdomen is compressed, the wings rather short. The pronotum elongate on dorsal surface, and the legs are rather short. However, in some ways it shows affinity with Sericopompilus; the stigma is long, as in Sericopompilus the anal vein of hind wings ends much before the cubital fork, and on the hind tibia there are a few spines of the median row.

Euplaniceps saussurei Kohl

Common in Chili.

Euplaniceps herberti Fox

From Kartabo, British Guiana, 16 May.

Euplaniceps pertyi Banks

From Kartabo, British Guiana, 13 April.

Euplaniceps lacordairei Guerin

From Nova Teutonia, Santa Catharina, Brazil, 30 September, 31 January (Plaumann).

Euplaniceps punctatus Bradley

From Santa Cruz, Bolivia (Steinbach).

Euplaniceps lotus spec. nov.

Male. Black, abdomen with a white spot on each side of second and third segments, widely separated, abdomen polished above; antennae dull brownish rufous; legs black, white spot at base of hind tibiae, spurs white, front tarsi paler. Wings hyaline, apical part beyond cells dark, extending into most of marginal and one-half of the second-third submarginal. Body more or less sericeous, especially prominent on propodeum, lower face, coxae below, and some on femora.

Clypeus broad and truncate below, ocelli in a very large broad triangle, laterals much nearer eyes than to each other; antennae very short, very thick, especially the joints toward base, these little longer than broad; pronotum angulate behind, in front sloping but little, wholly sericeous; propodeum short, from side evenly curved, covered above with sericeous pubescence; abdomen slender, rounded transversely, much less broad than thorax, somewhat compressed. Legs rather short, hind tibiae with the two rows of spines well developed and a row of smaller spines between them; inner spur almost as long as basitarsus.

Fore wings with the membrane densely covered with a criss-cross of short curved hairs as in male of *lucanus*; the marginal cell is small, slenderly triangular, with but two abcissae, the second in line with the third; first abcissa very short and but slightly oblique, the last abcissa (two, three and four) in a line much longer than costal length of cell, marginal cell about its length from wing-tip, the second and third submarginals united in one cell, which is about the length of marginal cell, first recurrent vein ends before end of basal third,

second recurrent (sinuous) ends a little before tip of cell; in hind wings the anal vein ends much before forking of cubitus.

Length of fore wing 5 mm.

One male from Santa Cruz, Bolivia (Steinbach). Type M.C.Z. no. 26702.

Euplaniceps bradleyi spec. nov.

Male. This male is similar in most respects to that of *E. saussurei* Kohl. Black; lower face, clypeus, and hind border of pronotum silvery pubescent, also mid and hind coxae, lower part of mesopleura, and an elongate silvery spot each side at tip of propodeum; spurs white. Fore wings beyond basal vein not as dark as *saussurei,* and no white band before stigma, however, the apical two-thirds of first submarginal cell, the apical part of first discoidal cell, and much of the third discoidal nearly hyaline, but together they make only a faint, irregular pale area.

The antennae are shorter than in *saussurei* the fourth and fifth joints each not twice as long as broad. Most noticeable is the almost complete absence of hair on head and pronotum, *saussurei* having much dark hair on these parts.

In the fore wings the second submarginal cell and the third discoidal are each longer than in *saussurei,* the latter with outer side not quite as long as lower side.

Length of fore wings 6.5 mm.

One from Campinas, Sao Paulo, Brazil, March (F. X. Williams). Type M.C.Z. no. 26773.

Subfamily NOTOCYPHINAE

This subfamily is represented in America by one genus only, Notocyphus.

The labrum is wholly exposed; no hairs nor bristles on basal parts of maxillae; no groove on second ventral segment of abdomen; in fore wings the first recurrent vein usually ends beyond the basal third of second submarginal cell, and no pocket in base of third discoidal cell; spiracle of propodeum twice its length from base of propodeum; legs with very small spines, hind tibiae never with teeth nor carinae above, claws cleft; inner margin of eyes not emarginate, face little narrowed below; no spines on under side of last joint of mid and hind tarsi.

Notocyphus is one of the most readily recognized genera in the Psammocharidae; the long labrum separates it from all; this projects a little backward from the edge of the clypeus. There is usually but little hair anywhere on body. The pronotum above is somewhat elongate in most females, sometimes more than one-half as long as mesonotum. The males and some females have the propodeum like most of the family, a fairly long posterior slope, and short basal part, but in many females the basal part reaches nearly to tip, and then drops suddenly, often with a concave area. The spiracles are placed further back than common, usually about one-half way back, and from the spiracle, a groove or furrow extends back to the outer corner of propodeum. Abdomen is slender, apical part compressed; the legs not especially long, fairly stout, and with at most very short spines; the tibiae are bordered at tip with very small, close-set stout spines; the claws are cleft. The venation is much as in the Cryptochilinae.

Most of the females have the propodeum with a long, even basal part which drops quite suddenly near tip of propodeum, this short apical part is often concave and the lateral corners projecting backward; a few species, two known to me, *procris* and *nubilipennis*, have a longer and sloping apical part, separated from the normal and shorter basal part, this also the condition in nearly all males.

The males usually have the pronotum quite long, and the hind margin but little arcuate; several species, however, *alboplagiatus*, *nessus*, *lucasi*, *adoletis*, *signatus*, *unicinctus*, and *rufigaster*, have the pronotum deeply and angulately emarginate behind, so that it is very short in the middle. In these the basal vein is interstitial or nearly so with the transverse; in other species the basal vein ends much before the transverse.

Three species, two females and one male, have distinct although small spines set in spine-pits on the underside of the hind femora; these are *saevissimus*, *thetis*, and *variegatus*.

The females can also be separated into two groups according to the ending of the basal vein; the following species have it almost one-half to fully one-half the length of transverse vein before the transverse vein: *melanosoma*, *williamsi*, *picticornis*, *inornatus*, *nigrinus*, *brevicornis*, *ferrugineus*, *aurantiicornis*, *vindex*, *thetis*, *pallidipennis*, *maculifrons*; in *saevissimus*, the type of the genus, *tyrannicus*, *procris* and *nubilipennis*, the basal vein ends at or very close to the transverse. But *procris* and *nubilipennis* differ greatly from *saevissimus* and *tyrannicus*, in the shape of propodeum, so that a subgenus based on either of these characters would hardly be natural; *bipartitus* is

intermediate. In the males several species have rufous to yellowish hind (sometimes others) femora, these are *adoletis, signatus, fraternus, unicinctus, morosus, lucasi,* and *dolorosus.* Turner (1915) says that *Agenia lactabilis* Sm., *A. conspicua* Sm., *A. ordinaria* Sm., *A. multipicta* Sm., *Ceropales fumipennis* Cam., *C. lugubris* Sm., *C. crassicornis* Sm., and *C. smithi* D. T. belong to Notochyphus.

Notocyphus

Females

1. Thorax and abdomen black, except possibly fifth or sixth segment paler 2
   Thorax or abdomen or both with pale marks besides extreme tip 9

2. Wings yellowish, wholly or in part 3
   Wings not plainly yellowish 5

3. Fully apical third of wings black; propodeum strongly concave at tip ..... *pictipennis*
   At most the dark beyond the closed cells 4

4. Wings darkened near tip; propodeum strongly concave at tip, the lateral angles projecting; stigma about twice as long as broad before radius ..... *melanosoma*
   Wings scarcely darker at tip, tip of long basal part of propodeum sloping, not concave nor any angles projecting; stigma not nearly twice as long as broad before radius; second recurrent ends beyond middle of cell ..... *williamsi*

5. Basal vein ends only a trifle before transverse vein; body and antennae very slender; propodeum concave at tip of long basal part ..... *tyrannicus*
   Basal vein ends fully one-half length of transverse before transverse 6

6. Tip of abdomen with pale spot on fifth or sixth segment 7
   Tip of abdomen black, unspotted 8

7. Sixth segment with pale spot; fore wings nearly evenly dark; indistinct pale spots on sides of second and third segments ..... *vindex*
   Fifth and sixth segments with pale spot; fore wings with paler areas; tip of long basal part of propodeum concave ..... *inornatus*

8. Propodeum with long basal part concave at tip; palpi dark; very large species ..... *nigrinus*
   Propodeum with a short basal part; posterior slope long and not concave; palpi pale except last joint ..... *brevicornis*

9. Head, thorax, abdomen, and legs almost wholly reddish; dark band at tip of first and second segments ..... *ferrugineus*
Head and thorax at least mostly black 10

10. Propodeum with a short basal part, and a longer sloping posterior part, not concave 11
Propodeum with long nearly level basal part, and a concave area at tip, often with ridge or angles projecting 12

11. Fore wings black; abdomen reddish on three segments, tip black, palpi pale ..... *procris*
Fore wings largely hyaline, tip darker; abdomen reddish in apical part, a pale spot each side on second segment; palpi pale ..... *nubilipennis*

12. Hind femora below with small spines arising from spinepits; palpi pale 13
No spines below on hind femora 14

13. Basal vein ends only a little before transverse; abdomen black on third and fourth segments, others mostly pale yellowish ... *saevissimus*
Basal vein ends one-half length of transverse before transverse; abdomen reddish on all segments; fore wings only smoky ..... *thetis*

14. Antennae mostly rufous; propodeum with an apical slope nearly one-half of basal part; wings dark brown ..... *aurantiicornis*
Antennae black 15

15. Abdomen mostly black, with rufous or whitish spots on sides of some segments 17
Abdomen largely rufous 16

16. Basal segment of abdomen black, others rufous; wings nearly hyaline; palpi pale ..... *maculifrons*
Basal segment rufous as the others; palpi darkened on base; wings dark brown, coppery iridescent ..... *bipartitus*

17. Abdomen with spot on each side of second and third segments and a median spot on sixth segment; clypeus pale, black spot in middle; wings black or nearly so ..... *vindex*
Abdomen with rufous spots on sides of second, third, and fourth segments, and a median one on sixth; wings very pale, very slightly yellowish ..... *pallidipennis*

Males

1. Thorax black, abdomen black, except small pale spot at tip; propodeum with dense, short, partly erect hair 2
Thorax and abdomen not wholly black 3

2. Clypeus wholly black, face also; mid furrow of propodeum weak; basal vein ends at transverse ..... *atratus*
   Clypeus with large pale spot each side; face with pale line on orbits; mid furrow of propodeum deep; basal vein ends plainly before transverse ..... *abnormis*

3. Thorax mostly rufous above; abdomen largely pale yellowish; face, clypeus, and labrum pale; wings yellowish; hind femora with spines in spine-pits beneath ..... *variegatus*
   Thorax black, or with some small pale marks 4

4. Abdomen mostly rufous, pale mark each side of third segment; hind border of pronotum and some spots on thorax whitish; lower face, clypeus, and labrum yellowish; wings nearly hyaline ..... *rufigaster*
   Abdomen not rufous, or only rufous spots, or yellowish on base 5

5. Thorax black, with some pale spots along middle, usually one on scutellum 6
   Thorax wholly black, no pale spots, except possibly some sericeous patches 11

6. All femora black 7
   Some femora rufous 8

7. Abdomen yellowish on most of first and second segments above, propodeum with three yellowish spots near tip, or in middle; a small dark cloud over marginal and third submarginal cells ..... *ornatus*
   Abdomen black on first and second segments; an interrupted pale band on third segment; propodeum with pale spot at each hind corner; no cloud in fore-wings, pronotum short in middle ..... *alboplagiatus*

8. All femora and some of coxae rufous 9
   At least front femora black 10

9. White band on third segment complete; no band on fore wings but tips dark; pale spots at tip of propodeum ..... *unicinctus*
   White band on third segment interrupted; a dark band over marginal cell and behind ..... *adoletis*

10. Both mid and hind femora at least partly rufous; no cloud in fore wings; pronotum pale behind ..... *lucasi*
    Only hind femora rufous; dark band on wings ..... *dolorosus*

11. Hind femora rufous, sometimes mid also 12
    All femora black 13

12. Hind femora rufous and mid partly; labrum black; wings nearly black; abdomen shining above ..... *fraternus*
Hind femora only rufous; labrum whitish; wings only smoky ... *signatus*

13. Abdomen with white spots on sides of second and third segments; wings black; labrum white; also pale spots on second and third ventral segments ..... *morosus*
No white spots on side of second segment, sometimes on third segment; labrum black 14

14. Pronotum short in middle, angulate behind, seen from side rounded into the plainly sloping front; palpi pale; wings mostly pale; third submarginal cell about as broad at top as the second; last abscissa of radius straight ..... *nessus*
Pronotum not much shorter in middle than on sides, seen from side the frontal part vertical 15

15. Body rather densely clothed with whitish pile or pubescence nearly all over; clypeus cream-white; apical fourth of front tibiae and the tarsi (except last joint) pale yellowish; no spot on third segment ..... *sericeus*
Body not noticeably sericeous; clypeus largely black; white spot on each side of third segment, hidden in retraction 16

16. Clypeus hardly more than twice as broad as long; labrum narrowed only slightly below, little longer than clypeus; third submarginal cell greatly narrowed above, not one-half of second ..... *sigmoides*
Clypeus fully two and one-half times as broad as long; labrum broad at base, much narrowed below, plainly longer than clypeus; third submarginal cell nearly as long above as second ... *deceptus*

Notocyphus saevissimus Smith

Females from Belem, Para, Brazil, June (Williams); Province Sara, Bolivia (Steinbach); Buenavista near Santa Cruz, Bolivia (Steinbach, Cornell Univ.), Campinas, Sao Paulo, Brazil, September (Williams).

Lower margin of clypeus hardly one-half of basal width; second plus third antennal joints nearly equal vertex-width; vertex rounded in even curve with top of eyes; pronotum more than two-thirds of mesonotum, in front vertical and faintly concave; basal part of propodeum fully equal to mesonotum, behind concave and the lateral angles projecting, the upper edge not notched in middle; first recurrent vein ends at about end of basal third, or a little before; third submarginal cell narrowed to one-third above, outer side strongly bent, second recurrent ends before middle.

Length of fore wing 7.5 mm to 15 mm.

NOTOCYPHUS SAEVISSIMUS var. INDENTATUS var. nov.

Female differs from *saevissimus* in that the first abdominal segment is black on basal half and the fifth segment (as well as third and fourth) also black; the propodeum is deeply indented in the middle of the terminal ridge of basal part; second plus third antennal joints plainly not equal to vertex width.

Length of fore wings 12 mm.

From Province Sara, Bolivia (Steinbach); type M.C.Z. no. 26869.

NOTOCYPHUS TYRANNICUS Smith

Female. Body, legs, antennae deep black; wings dark brown, paler toward tips, iridescent, veins black. Body as slender as in *N. saevissimus*, antennae longer and more slender; clypeus about three times as broad as long, labrum much longer, slightly tapering to the scarcely concave tip; second plus third antennal joints fully equal vertex-width; front, vertex, and cheeks with much rather long hair, front coxae also very hairy much as in *N. abnormis*; lateral ocelli fully as near to eyes as to each other, a groove from each ocellus to eye; pronotum moderately long, but shorter than in *saevissimus*, nor are the sides as sharply produced as in that species, with rather short hair on sides; propodeum slender and long as in *saevissimus*.

Abdomen slender, basal segment about as long as broad behind, last segment above with few very fine short hairs. Legs much as in *saevissimus*, inner spur of hind tibia about one-half of basitarsus; inner tooth of claw thick, but with a sharp point.

In the fore wing the marginal cell is not nearly as broad as the submarginals; second submarginal cell nearly twice as long below as broad, base much sloping, tip but little sloping, receiving the first recurrent vein near middle; third submarginal cell fully as long below as second, above narrowed more than one-half, outer side sloping, then angularly bent, and in both wings with an outer stub-vein, receiving the second recurrent vein (curved) at middle; basal vein almost interstitial with transverse, lower section slightly bulging toward base; in hind wings the anal vein ends much beyond the forking of cubitus.

Length fore wings 17 mm.

One from Iquitos San Rogue, Peru, April 1929 (Klug coll.); others from Blairmont, British Guiana, 24 October (F. X. Williams).

NOTOCYPHUS WILLIAMSI spec. nov.

♀ A yellow-winged species, not darkened at tip; body black, tip of abdomen slightly yellowish; in one (small) specimen the second segment is mostly dull rufous, and third segment with large, dull rufous area each side; on larger specimen there is only a faint rufous spot on each side of the second segment; a short yellowish streak on inner orbits above antennae and another higher up, on the posterior orbit. The clypeus shows more or less distinctly a rufous tinge each outer side, and the labrum also has a rufous tinge at each upper outer corner; the palpi are yellowish, the clypeus, and head in general similar to *saevissimus*, frontal groove complete, the vertex, however, somewhat more narrow, and the ocellar triangle less broad, the hind ocelli, however, as near eyes as to each other; antennae rather short and thick; the second plus third joints are nearly equal to vertex-width. From side the pronotum curves into the not quite vertical front, the dorsal part almost half the mesonotum, latter scarcely arched. From side the propodeum is nearly level for more than one-half its length, there ending in a flattened slope, somewhat triangular. Abdomen slender, compressed at tip; on mid tibiae there are many short spines above as well as below, but not so numerous as in some species; on hind tibiae no distinct spines above, but a few faint ones on sides and below; the front tibiae are bordered at tip with minute closely set spines much as in *saevissimus*, inner spur of hind tibia slightly curved, and nearly one-half of basitarsus.

Venation similar to *saevissimus*; the basal vein at same distance before transverse; the second sub-marginal cell short and less narrowed above, the first recurrent ends near middle; third submarginal cell with outer side curved at turn (not angled), the second recurrent ends at forking of cubitus; stigma a little longer than in *saevissimus* and the tip more oblique.

Length of fore wings 9.5 mm. and 15 mm.

Two females from Tena, Ecuador, 23 February, 16 March (F. X. Williams). Type M.C.Z. no. 26818, paratype with Mr. Williams).

NOTOCYPHUS NIGRINUS spec. nov.

♀ Black throughout, no paler marks, palpi dark, wings iridescent bluish; body proportionally broader and heavier than *tyrannicus*, antennae with the joints as long but much thicker. Clypeus a little longer than in *tyrannicus*, and the labrum narrowed to less than one-half of basal width, head much thicker especially behind eyes

where it extends back almost the width of ocellar area (in *tyrannicus* not one-half as far); front and vertex with very short hairs (twice as long in *tyrannicus*); pronotum as long as in that species but faintly angulate behind (arcuate in *tyrannicus*); propodeum with the level part as long as in that species, but broader, with the turn not so plainly ridged, the lateral angles projecting slightly; abdomen broader, not polished, legs, especially the femora, thicker than in *tyrannicus*; front coxae with only very short hair; mid and hind tibiae with short spines, some above, several rows above on mid tibiae, inner spur of hind tibiae not one-half of basitarsus. The front wings are fairly broad; the marginal and submarginal cells much as in *tyrannicus*, the outer side of third not angled; first recurrent vein ends further beyond middle and the second recurrent ends more nearly to middle, the basal vein ends more than one-half length of transverse vein before that vein; in hind wings the anal vein ends much nearer to fork of cubitus.

Length of fore wings 22 mm.

From Province Sara, Bolivia (Steinbach); Buenavista near Santa Cruz, Bolivia (Cornell). Type M.C.Z. no. 26824, paratype at Cornell Univ.

Notocyphus melanosoma Kohl

A female from Villarica, Paraguay, January (F. Schade). Labrum long, lower edge less than one-half of upper; second plus third antennal joints about equal vertex-width; vertex roundedly elevated above eyes, hind ocelli further from occiput than from each other or from eyes; pronotum and mesonotum evenly arched above head; pronotum in middle about half the length of mesonotum, in front vertical; basal part of propodeum hardly more than one-half of mesonotum, broadly, deeply concave behind, lateral angles projecting; hind tibiae with a few spines above and below, inner spur not quite one-half of basitarsus; in fore wings marginal cell very long and slender, fully six times as long as broad, (6 mm. long, not 1 mm. wide), last abscissa not nearly equal to second abscissa plus third, second submarginal cell more than one and one-half times as long as broad, base much more oblique than tip, first recurrent ends in middle; third submarginal cell one-half longer below than second, narrowed one-half above, receiving second recurrent (nearly straight) before middle; basal vein ends much before transverse; in hind wings the anal vein ends much beyond forking of cubitus.

Notocyphus pictipennis var. nigricornis var. nov.

A female from Maracajú, Matto Grosso, Brazil, April-May 1937 (G. Fairchild).

This agrees well with the description of *pictipennis* by Fox, except that the last seven joints of antennae are not orange but black as the others. Labrum with sides slightly concave, tip almost one-half of base; second plus third antennal joints nearly equal vertex-width; front with a very deep median groove, pronotum behind in middle not two-thirds of mesonotum, propodeum in middle about as long as mesonotum, tip not deeply concave, and only slightly angled, ending almost directly above end of propodeum; in front wings first recurrent ends beyond middle of cell; third submarginal cell with outer side strongly angled, top equal top of second, and one-third of lower side, second recurrent vein (bent in middle) ends barely beyond middle of cell.

Type M.C.Z. no. 26585.

Notocyphus maculifrons Smith

A female from Iquitos, San Rogue, Peru, Febr. 1929, (Klug coll., Cornell Univ.). It is marked as compared with type by Dr. Babiy.

The lower margin of clypeus is fully one-half of upper margin; pronotum in front nearly vertical, above about two-fifths of mesonotum, arcuate behind; tip of propodeum very much as in *vindex*; hind tibiae show few spines, inner spur one-half of basitarsus. Marginal cell with last abscissa about equal to second plus third; second submarginal cell quite long, base hardly more oblique than tip; first recurrent vein ends much before middle; third submarginal rather short, but little longer below than second, much narrowed above, second recurrent (not strongly bent) ends beyond middle.

Notocyphus vindex Smith

A female from Iquitos, Peru, (H. Bassler) (Amer. Mus. Nat. Hist.); also Kaieteur, British Guiana, 11 August (Cornell). This specimen marked "compared with type" by Dr. Babiy. The Iquitos specimen has the marks on abdomen smaller and more rufous and hind wings are darker but both have the dark spot on the pale clypeus.

The palpi are pale; clypeus about two and one-half times as broad as long, labrum with lower margin about one-half upper; hind ocelli

about as near eyes as to each other, pronotum about one-half of mesonotum, arcuate behind; legs rather short, mid tibiae slightly thickened, above with many small spines, hind tibiae with few spines above and below, inner spur almost equal to half the basitarsus.

In fore wings marginal cell acute at tip, as broad as submarginals, second submarginal is hardly one-half longer below than broad, about half as long above, receiving first recurrent before middle; third submarginal cell fully one-half longer below than second, narrowed one-half or more above, receiving the second recurrent vein at middle; basal vein ends fully one-half of transverse vein before transverse; in hind wing anal vein ends at forking of cubitus.

Notocyphus aurantiicornis Lucas

A female from Passo Fundo, Rio Grande do Sul, Brazil, 8 January, 1920 (Cornell Univ. Exped.).

Labrum not very long, lower edge hardly one-half of base; antennae short, rufous, but joints 1, 2, 10, 11, and 12 black; second plus third not nearly equal vertex-width; vertex slightly rounded between eyes; hind ocelli much nearer eyes than to each other; pronotum vertical in front, about two-fifths of mesonotum; basal part of propodeum about one-half of mesonotum, the tip sloping, barely concave; marginal cell about as in *saevissimus*; second submarginal cell has base no more oblique than tip, first recurrent vein ends beyond middle; third submarginal cell only a little longer below than second, narrowed above almost to a point, second recurrent vein (bent in upper part) ends a little before middle; basal vein ends much before transverse; in hind wings anal vein ends a little beyond the forking of cubitus; hind tibiae with many small spines; inner spur almost one-half of basitarsus.

Notocyphus brevicornis Fox

A female from Huanuco, Peru, August (R. Ferreyra).

Labrum rather short, lower margin about one-half of base; pronotum above not one-fourth of mesonotum, broadly arcuate behind; basal part of propodeum not equal to mesonotum, tip sloping, not concave. Hairy; front with much erect black hair, also shorter hairs on pronotum, pleura with much short, fine hairs, clypeus with long, very fine pale hairs, tip of abdomen more hairy than usual. In fore wings first recurrent vein ends near middle of cell, third cell but little longer

than second, top hardly equal to second, about one-third of lower side, outer vein almost bent, second recurrent (plainly curved) ends a little beyond middle.

Notocyphus ferrugineus Fox

One female from Province Sara, Bolivia (Steinbach).

Labrum short, lower edge fully one-half of upper; frontal groove not very distinct; second plus third antennal joints equal vertex-width; pronotum in front hardly vertical, rounded into upper part, this fully one-third of mesonotum; propodeum with the basal part more than one-half of mesonotum, the posterior slope a little shorter, scarcely concave; spines on mid and hind legs short but stout, and quite prominent, inner spur of hind tibiae more than one-half of basitarsus; front quite hairy, but much shorter hairs on pronotum.

In fore wings the basal vein ends near to transverse; second submarginal cell short, narrowed above, first recurrent ends much beyond middle; third submarginal one-half longer below than second, end almost angled, second recurrent (hardly curved) ends at middle.

Notocyphus pallidipennis spec. nov.

♀ Body dull black, legs black, tarsi brown, antennae mostly brown, clypeus and labrum wholly brown; palpi pale, abdomen with rufous spots on sides of second, third, and fourth segments, those on third segment nearly meeting above, also a median spot on sixth segment; wings nearly hyaline, faintly yellowish, veins and stigma yellowish to ferruginous.

Clypeus fully three times as broad as long, labrum one and one-half times as long as clypeus, lower margin more than one-half of upper, slightly concave, and the sides also concave in middle; frontal groove complete; hind ocelli about as near eyes as to each other; second plus third antennal joints a little more than vertex-width; pronotum in middle fully one-half as long as mesonotum, rounded into sloping frontal part. Propodeum almost as long as the mesonotum, concave behind, lateral angles projecting, a median groove on posterior part of the basal part; spiracles nearly one-half way back, the deep groove ends in a very large pit.

Abdomen rather broad at base, tip with erect pale hair; mid tibiae slightly swollen, with many very small spines above, hind tibiae with

a row of short spines on upper outer side, others on lower sides; inner spur not quite one-half of basitarsus.

In fore wings the marginal cell is long and slender, not as broad as submarginals, last abscissa outwardly a little concave; stigma short; second submarginal cell fully one and one-half times as long below as broad, above nearly one-half shorter, receiving the first recurrent vein a little before middle; third submarginal cell nearly one and one-half times as long below as second, upper side more than one-half of lower, receiving second recurrent (strongly bent above middle) at middle; basal vein ends more than one-half length of transverse before the transverse vein; in hind wings the anal vein ends at forking of cubitus.

Length of fore wings 16 mm.

One female from Rio Santiago, Peru, 15 to 28 December (H. Bassler), Amer. Mus. Natural History.

Notocyphus inornatus spec. nov.

♀ Body, legs, antennae, and wings black; apical part of fourth and all of fifth and sixth segments rufous; palpi pale; fore wings with an irregular pale area behind stigma into basal part of third discoidal cell; hind wings smoky, basal part clearer; each side of scutellum there is a small triangular patch of white pubescence.

Clypeus nearly two and one-half times as broad as long, labrum longer than clypeus, tapering to the tip about one-half as long as base, lower margin with a median indentation; face moderately narrow, frontal groove distinct; hind ocelli fully as close to eyes as to each other. Antennae moderately short, second plus third joints nearly equal vertex-width; pro and mesonotum arched above head, pronotum vertical in front, above fully two-thirds of mesonotum, not as long as in *saevissimus*; propodeum from side elongate and level above for a distance equal to basal width, not quite as long as in *saevissimus*, the lateral angles project slightly, and between concave, but not quite as near vertical as in *saevissimus*, the basal part has a distinct median groove.

Abdomen as slender as in *saevissimus*, and compressed toward tip; the front tibiae are bordered at tip with close-set spines as in *saevissimus*, but shorter; mid tibiae have numerous short spines above and on sides; hind tibiae have a row of short spines above, another row along upper outer side, smaller on sides and below, inner spur of hind tibiae hardly one-half of basitarsus.

In fore wings the marginal cell is not as long nor as slender nor as acute at tip as usual, the last abscissa being outwardly convex; stigma rather long, mostly before origin of radius, tip oblique; second submarginal cell longer below than broad, base more oblique than tip, about as in *williamsi*, first recurrent ends before end of basal third; third submarginal much longer below than second, not above, outer side strongly bent on lower part, receiving the second recurrent (scarcely curved) a little before middle; basal vein ends farther before transverse than in *saevissimus*; in hind wings the anal ends at forking of cubitus.

Length of fore wing 11 mm.

One female from Rio de Janeiro, 29 January (F. X. Williams). Type M.C.Z. no. 26817.

Notocyphus bipartitus spec. nov.

♀ Black; labrum becoming rufous to brown below; palpi yellowish; antennae rather brownish below; abdomen entirely dark rufous, last segment paler; legs black; wings brown, iridescent, veins mostly black.

Body slender; tip of abdomen strongly compressed. Clypeus moderately long (about as in *saevissimus*), labrum but little if any longer, tapering somewhat to the broad and truncate tip; face moderately narrow, scarcely narrowed above; frontal groove scarcely visible except at each end; hind ocelli nearer to eyes than to each other; second plus third antennal joints equal to vertex-width; pronotum about two-thirds as long as mesonotum, slightly arcuate behind, in front vertical; propodeum long, level to the concave tip, not quite as vertical as in *saevissimus*, within the concavity the surface is transversely striate, the lateral angles project a little. Abdomen slender, smooth and polished, last segment and last few ventrals with some pale hair. Front tibiae at tip with short spines, not as close set as those in *saevissimus*; mid tibiae with many short spines above, hind tibiae with a row above and more on sides, inner spur fully one-half of basitarsus.

In the fore wings the marginal cell is very long and acute at tip; stigma very short, entering cell only a little, tip oblique; second and third submarginal cells much as in *saevissimus*, second rhomboidal, scarcely narrowed above, receiving the first recurrent vein before middle; third submarginal cell longer than second, receiving the second recurrent (very sinuous) a trifle before middle, outer end strongly oblique and then bent below middle; basal vein ends plainly

before transverse; in hind wings the anal vein ends at forking of cubitus

Length of fore wing 14 mm.

One female from Naranjapata, Ecuador, 1850 ft., December, (F. X. Williams); type M.C.Z. 26819.

Notocyphus procris spec. nov.

Female. Black on head, thorax, legs, and antennae; wings blackish, somewhat paler at tip; abdomen with first, second, and third segments reddish above and below, other segments black; palpi yellowish, a small patch of yellowish hair below base of each antenna, a faint yellowish spot on middle of metascutellum; spurs yellowish brown.

Clypeus about two and one-half times as broad as long, labrum long, tapering slightly to the slightly concave tip, each outer corner faintly pale; face with median line; third antennal joint not quite equal to vertex width; hind ocelli about as close to eyes as to each other; pronotum short, not as long as vertex, almost angulately emarginate behind; propodeum as broad at base as long, anterior part a little rounded, and rounded into posterior part, which is nearly flat transversely.

Abdomen moderately long, somewhat compressed toward tip, first segment not as long as broad at tip; inner spur of hind tibia about one-half of basitarsus. In fore wings the marginal cell as broad as the second submarginal cell, latter about one and one-half times as long as broad, both ends equally sloping, receiving the first recurrent vein plainly beyond middle, third submarginal a little longer below than second, only about one-third as long above, outer side strongly bent near middle, receiving the second recurrent a little beyond middle; basal vein almost interstitial with transverse; in hind wings the anal ends at forking of cubitus.

Length of fore wings 11.5 mm.

One from Maracajú, Matto Grosso, Brazil, April-May (G. Fairchild). Type M.C.Z. no. 26586.

Differs from *N. bicolor* in having frontal groove, shorter inner spur of hind tibia, first recurrent ends beyond middle of cell, and both submarginals shorter; probably in other points.

Notocyphus nubilipennis Fox

One female from Jatun Nacu, Rio Napo watershed, Oriente, Ecuador, 700 m. (W. C. MacIntyre).

Labrum rather short, tip about one-half base, frontal groove deep near ocelli; second plus third antennal joints equal vertex width, vertex little rounded; front with much erect dark hair, a little on pronotum and some on pleura; pronotum in front plainly sloping, above in middle hardly more than one fourth of mesonotum; propodeum with long posterior slope rounded into the much shorter basal part.

In fore wings basal vein ends close to transverse, the second submarginal not as long as high, first recurrent ends at middle; third submarginal cell almost twice as long below as second, one-half as long above, outer side angled, second recurrent (slightly curved) ends in middle of cell.

NOTOCYPHUS SIGNATUS spec. nov.

Male. Black; clypeus and labrum whitish, a broad white streak on orbits up to middle of face; basal antennal joint below whitish, antennae dark brown, pronotum narrowly bordered behind with white, sometimes absent, a white spot each side in front, rather low down; legs black, front tibiae and tarsi yellowish, hind femora (except extreme tip) rufous, all coxae with silvery gray pubescence, propodeum with a minute whitish spot each side at tip, tip of abdomen faintly rufous; wings nearly hyaline to faintly smoky, hind ones paler, veins brown.

Clypeus nearly three times as broad as long, labrum longer, slightly tapering to truncate tip; antennae thick, short, finely incised between joints, third joint shorter than fourth, third, plus fourth and fifth joints hardly equal vertex-width; lateral ocelli little nearer to eyes than to each other; pronotum short in middle, arcuate behind, propodeum sloping to tip, broader than long; legs rather slender, inner spur of hind tibiae fully two-thirds of basitarsus; basal abdominal segment broader behind than long.

In the fore wings the marginal cell scarcely broader than third submarginal; second submarginal cell about one and one-half times as long below as broad, base much sloping, apex but little, receiving the first recurrent a little before middle; third submarginal cell plainly longer below than second, above not one-half of lower side, apical vein sloping at first then bent near middle, receiving the second recurrent about at middle; basal vein ending near transverse, lower section erect and only slightly curved, not sloping; in hind wings anal ends at forking of cubitus.

Length of fore wings 6 mm.

From La Sombra, Peru, 22 August (Cornell Univ. Exped.). Type at Cornell Univ., paratype at M.C.Z. no. 26592.

Notocyphus alboplagiatus Smith

A male from St. Augustine, Trinidad, 21 June (N. A. Weber). Labrum fairly long, sides concave, tip fully one-half base; frontal groove quite deep above, front rather hairy, hairs not long; vertex but little rounded, antennae somewhat crenulate, pronotum sloping in front, rounded into short upper part; propodeum from base to tip in a slightly curve slope; in fore wings the second submarginal cell is short, hardly one-half as long above, first recurrent ends near middle, third submarginal one-half longer below than second, above scarcely longer than second above, outer side strongly rounded at bend, second recurrent (nearly straight) ends beyond middle.

Notocyphus ornatus spec. nov.

Male. Head black, face yellowish almost up to the ocelli, a yellow line behind each eye, clypeus yellow, labrum brown, narrowly yellowish on margins; palpi pale yellowish, antennae brown (broken) first and second joints yellowish below; upper part of pronotum yellowish, a small yellowish spot on front edge of lower lobe, tegulae yellow; a spot on middle of mesonotum, near hind border, a triangular spot on scutellum, a band over post-scutellum, propodeum with three spots near hind border, the middle one slightly more forward than others, all yellowish. Basal segment of abdomen yellow below and largely above, the base and a band before hind border black; second segment with a large black spot above, full width behind, narrowed to one-half in front, the sides, narrow hind margin, and venter of second segment yellow; third segment above mostly dark, on sides in front yellow, venter dark, fourth and fifth segments dark above and below, sixth segment pale yellowish.

Legs black, coxae below silvery, front tibiae and tarsi yellowish, mid tibiae slightly rufous, hind legs wholly dark. Wings yellowish hyaline, marginal and third submarginal cells brown, veins and stigma also brown.

Hardly any hair on body; some short on upper front and vertex and on upper mesopleura.

Clypeus rather long, scarcely more than twice as broad as long; labrum about one-third longer than clypeus, tip less than one-half as long as base and concave; frontal groove incomplete, hind ocelli as

near eyes as to each other; third antennal joint a little more than twice as long as broad; pronotum vertical in front, rounded to upper part, latter hardly one-third as long as mesonotum, hind margin broadly arcuate; propodeum fully as long as broad at base, sides parallel, from side sloping with little curve from base to tip. Abdomen rather broad, not flattened; legs with few spines, hind tibiae with distinct, but short spines on under side, above with very short and fine ones.

In fore wings the marginal cell fully half its length from tip of wing, as broad as the submarginals; stigma with a rather long, oblique tip in the cell; second submarginal cell a little longer below than broad, narrowed above to nearly one-half, receiving the first recurrent vein a little beyond middle; third submarginal cell longer below than second, narrowed to hardly one-half above by the sloping base and more sloping tip, latter much bent on lower part, receiving the second recurrent vein (nearly straight) plainly beyond middle; basal vein ends a little before transverse, lower section bulging basally; in hind wings the anal vein ends scarcely beyond forking of cubitus.

Length of fore wings 11 mm.

One male from Bucay, Ecuador, 1,000 ft., 4 October (F. X. Williams). Type M.C.Z. no. 26821.

A female from the same locality and date is very similar in the yellowish markings, except that there is but a median spot at end of propodeum instead of the three in the male, and the spots on sides of first and second segments are not so large and do not extend much on the upper side, and that on the second segment is confined to the basal half, there is also a smaller spot on side of third segment, and the last dorsal segment is yellowish.

The antennae are black, except for the basal joint below, and the front tarsi are yellowish to almost rufous. The wings are the same and also the venation. In the female the face is broader, and broader at vertex than below; second plus third antennal joints not quite equal vertex-width, from in front the vertex is slightly rounded from between eyes; the hind ocelli almost as near eyes as to each other.

The propodeum (from side) nearly evenly sloping from base to tip, much as in *brevicornis*, a very distinct median groove on basal part, each anterior corner with silvery pubescence, which is also on pleura and coxae; hind tibiae with numerous spine-pits, also on mid tibiae, each with a tiny spine; inner spur of hind tibia fully two-thirds of basitarsus.

Length of fore wings 12 mm.

Notocyphus unicinctus Brèthes

Several males from Tucuman, Argentina (Reed) Cornell lot 605. The original description is quite short.

Black, clypeus, and the usual face marks white, the labrum usually mostly dark, or pale on sides, a dark spot on middle of clypeus, sometimes very broad; antennae black, only a little paler on scape beneath; hind border of pronotum, spot on side of pronotum, at end of mesonotum, one on scutellum, another on post-scutellum white; an elongate spot each side at tip of propodeum, so long they almost or quite meet in middle, a silvery circle each side on basal part of propodeum; abdomen with a rather broad band across base of third segment and extreme tip above white. Legs mostly yellowish to rufous, front coxae black, others rufous, the hind tarsi nearly black beyond basitarsus. Wings hyaline, tips of fore pair darker, veins brown.

Body slender; clypeus about two and one-half times as broad as long, labrum longer, tapering to a slightly concave tip; front and vertex with rather dense short hair; third joint of antennae hardly twice as long as second, shorter than fourth; ocelli as near eyes as to each other; pronotum very short in middle above; propodeum slopes to tip, rather broader at base than long; abdomen slender, basal segment almost as long as broad at tip; legs slender, inner spur of hind tibia about one-half of basitarsus, no spine-pits under femora.

In fore wings the marginal cell is fully as broad as the submarginals; second submarginal about one and one-half times as long below as broad, from one-third to one-half as long above, apical vein sloping, receiving the first recurrent vein near middle; third submarginal cell as long below as second and longer above than second, maybe twice as long, outer side bent near middle (one specimen with a stub-vein), receiving the second recurrent near middle; basal vein interstial with transverse, lower section lightly curved toward base, not sloping; in hind wings the anal vein ends a little beyond forking of cubitus.

Length of fore wing 6 mm.

Notocyphus abnormis Taschenberg

A male from Chapada, Brazil (H. H. Smith coll. ex. Carnegie Museum).

Labrum long, lower side less than one-half basal, front densely, coarsely punctate, and with much erect hair, pleura and pronotum

also hairy; propodeum sloping as usual in males, apical part densely covered with erect, quite long brown hair; venation much as in *brevicornis,* but the basal vein ends barely before transverse.

Notocyphus variegatus spec. nov.

Male. Head yellow, a large black spot on vertex coming up from occiput covering ocelli and extending triangularly down about one-third way to antennae, latter rufous; prothorax and front legs wholly pale yellowish, mesonotum, scutellum, and metanotum also yellowish, mesopleura yellowish above; basal third of propodeum black, beyond and the pleura yellowish; abdomen mostly yellowish above, wholly on first, second, and sixth segments, the third, fourth, and fifth with a broad median dark mark, not black, but rather silvery gray, venter mostly dark, hardly black, sides of first and second segments somewhat yellowish; mid and hind legs (including coxae) black, except that the mid tibia and tip of mid femur above are yellowish to rufous, spurs of hind tibia brown, mid and front spurs more pale. Wings slightly yellowish, covered with very fine black hair, veins black; hind wings hyaline.

Clypeus about twice as broad as long, labrum little longer, tapering to the truncate tip. Median groove on front; hind ocelli nearer to eyes than to each other; third antennal joint about equal to first, third plus fourth longer than vertex-width. Pronotum about one-half length of head, arcuate behind, scutellum elevated and slightly compressed; propodeum broader than long, sloping to tip, each outer corner above hind coxae has a small cavity. Legs rather slender, inner spur of hind tibia fully one-half of basitarsus, under hind femora are numerous spine-pits, and some under mid femora; the bifid claws have the inner tooth about as long as outer one in mid and hind legs.

In the fore wings the marginal cell is broader than the submarginals; the second submarginal more than one and one-half times as long below as broad, the base slopes to narrow the cell to nearly one-half above, tip but little sloping, receiving the first recurrent vein plainly before middle; third submarginal cell about as long below as second; the top only one-third as long as bottom, apical vein much bent at end of second third; basal vein ends only a little before transverse vein, the lower section of basal vein is erect or a little sloping toward base; in hind wing the anal vein ends scarcely beyond the forking of cubitus.

Length of fore wing 12 mm.

One from Belem, Para, 19 Sept., 1924 (Bequaert). Type M.C.Z. no. 26587.

NOTOCYPHUS DOLOROSUS spec. nov.

Male. Black; labrum, clypeus, lower face, and up on each inner orbit, and line behind each eye, white to cream; basal joint of antennae below also pale; front coxae in front, mid coxae partly beneath, and hind coxae on side and tip, white; palpi pale; hind border of pronotum, long spot on middle of mesonotum, spot on scutellum, and spot each side at tip of propodeum, white; abdomen brown, with an interrupted white stripe across base of third segment, and a spot above on sixth segment, white; hind femora rufous except at each end; front tibiae and tarsi (except tip) yellowish, spurs dark; wings hyaline, a brown cloud over most of marginal and the third submarginal cells, veins brown. Clypeus fully two and one-half times as broad as long, labrum a little longer than clypeus, narrowed to nearly one-half below; ocelli rather large, hind ones closer to eyes than to each other, from each hind ocellus a broad groove extends to eye; antennae somewhat crenulate, quite short, neither third nor fourth joint twice as long as broad; pronotum very short in middle, hardly any real dorsal part there, deeply arcuate behind, in front nearly vertical. Propodeum tapering a little behind, nearly as long as mesonotum; pleura and sides of propodeum sericeous; legs moderately long, hind and mid tibiae with some very short spines, inner spur of hind tibiae two-thirds of basitarsus, of mid tibiae five-sixths of basitarsus. Fore wings with marginal cell rather short, stigma fairly long, longer than first abscissa; second submarginal cell narrowed one-half above, receiving the first recurrent vein near middle, third submarginal cell shorter than usual, narrowed fully one-half above, outer side abruptly bent, receiving the second recurrent (slightly bent) scarcely before middle; basal vein ends at transverse, last section nearly vertical at first but curved above; in hind wings anal vein ends a trifle before forking of cubitus.

Length of fore wing 9 mm.

One from Para, Brazil 29 July, 1919. Type in Amer. Mus. Nat. Hist.

Differs from *N. alboplagiatus* in rufous hind femora, entirely white front coxae, shorter and blunter marginal cell, shorter third submarginal and shorter antennal joints. From *N. signatus* it differs in having white marks on thorax and propodeum.

NOTOCYPHUS MOROSUS spec. nov.

Male. Body black, in some places with bluish iridescence; palpi dark, tips of some joints pale, mandibles white above, antennae and legs black, no pale marks on thorax nor propodeum, except a white spot each side on prosternum; abdomen with a fairly large white spot each side on second segment, a white band, interrupted in middle across base of third segment, seventh segment white; venter with whitish spot each side on second and third segments, those on the second being very small, and the subgenital plate white; fore wings dark brown, iridescent coppery, hind wings paler, but only basal lobe hyaline, veins brown to black. Body sericeous, strongly on face and lower front, on lobes of pronotum, mesopleura, all coxae, sides and basal and apical corners of propodeum.

Clypeus little more than twice as broad as long; labrum little longer than clypeus, narrow and rounded at tip; front slightly concave in middle; hind ocelli hardly nearer eyes than to each other; pronotum rather short, only slightly arcuate behind, rounded into frontal part, which, from side, is almost concave; propodeum longer than broad at base, longer than mesonotum, finely striate above; second segment of abdomen as broad as propodeum; mid and hind tibiae with short spines, some in a row above, inner spur of hind tibiae nearly two-thirds of basitarsus.

In fore wings marginal cell moderately long, slender and acute at tip, not as broad as second submarginal, last abcissa straight, stigma further in cell than before radius; second submarginal cell but little longer below than broad, narrowed hardly one-fourth above, receiving the first recurrent vein at middle, third submarginal cell only a little longer below than second, narrowed over one-half above, receiving second recurrent (nearly straight) at middle; basal vein ends just before transverse, vertical; in hind wings anal vein ends barely beyond forking of cubitus.

Length of fore wings 11 mm.

One from Cartagena, Colombia 1 January 1921. Type in Amer. Mus. Nat. Hist.

NOTOCYPHUS ATRATUS spec. nov.

Male. Body, legs, antennae deep black throughout, only sign of pale is basal part of last dorsal segment. Wings dark brown, but paler toward tip, veins black. Clypeus nearly two and one-half times as broad as long, labrum much longer, slightly tapering to

truncate tip; antennae short, second plus third plus fourth joints hardly equal vertex-width, vertex and front rather densely hairy, lateral ocelli about as near to eyes as to each other; pronotum about one-half as long in middle as length of head, as hairy as vertex above and on lower sides, mesopleura also hairy; propodeum broader at base than long, from side a rather even curve to tip, hairy on sides; abdomen rather short, basal segment hardly as long as broad behind, a few very short hairs at tip of abdomen.

Fore wing with marginal cell as broad as submarginals; second submarginal cell a little longer below than broad, base strongly oblique, tip less so, receiving the first recurrent vein a little beyond middle; third submarginal cell a little longer below than second, outer side sloping and beyond middle strongly bent, receiving the second recurrent vein near middle; basal vein ends a trifle before transverse, lower section sloping some and bulging a little toward base; in hind wing anal ends plainly a little beyond forking of cubitus.

Length of fore wings 10 mm.

One from Villarica, Paraguay, Sept. 1937 (F. Schade). Type at Cornell Univ.

Notocyphus fraternus spec. nov.

Male. Similar to *N. signatus*; body black, antennae and legs also, hind femora rufous, mid femora almost rufous on apical half; wings dark brown, iridescent; clypeus black, a large yellowish spot each side, and a triangular spot extending up each inner orbit to antennae, and then curving in to margin antennal socket from above, labrum black, palpi pale; abdomen polished above. Front and vertex with much long, erect black hair, also on pleura, short hair on basal segment of abdomen above, coxae below with dense white pubescence.

Clypeus fully two and one-half times as broad as long, labrum about one and one-half times as long as clypeus, lower margin not one-half of upper; frontal groove complete, hind ocelli scarcely nearer to eyes than to each other, antennae rather short, third joint not twice as long as broad. Pronotum sloping a little in front, rounded to upper part, which in middle is scarcely one-fourth of mesonotum, but longer than in *signatus*, hairy above, mesonotum also with short hair; scutellum and postscutellum elevated and compressed, and hairy above as in *N. abnormis*; propodeum from side an almost even slope, but little curved, above with dense very short erect hair; abdomen short and slender; mid and hind tibiae with spines and

bristles, long spur of hind tibia more than one-half of basitarsus, front basitarsus longer than next three joints together. In fore wings marginal cell is slender, acute at tip, hardly one-half its length from wing-tip, stigma quite long, projecting nearly as much into marginal cell as before it; second submarginal cell a little longer below than broad, narrowed above by slope of base, receiving the first recurrent a little beyond middle; third submarginal cell a little longer below than second, not much narrowed above, the outer side angled, but little sloping, receiving the second recurrent (nearly straight) plainly before middle; basal vein interstitial with transverse, in hind wing the anal ends at forking of cubitus.

Length of fore wing 10 mm.

One male from Banos, Oriente, Ecuador, 29 December (F. X. Williams). Type M.C.Z. no. 26820.

Differs from *N. signatus* in black labrum, partly black clypeus, darker wings, very hairy head, and hair on pleura.

Notocyphus sericeus spec. nov.

Male. Body black, densely clothed with whitish pile and pubescence nearly all over; thorax above, more strongly on pleura and coxae, propodeum silvery; abdomen less strongly sericeous, femora and tibiae partly so, also labrum, but scarcely any on front and vertex; palpi yellowish; clypeus cream-white, with a small black spot on middle of lower front margin, extending up on each side on lower face, not quite as high as ocelli, a narrow pale line behind eyes, hind border of pronotum with a narrow yellowish line, tegulae testaceous, antennae and legs mostly black, basal joint of antennae yellowish beneath; front tibiae on apical fourth and the tarsi (except last joint) yellowish; wings hyaline, with a bluish iridescence, slightly brownish toward tip, veins and stigma dark brown. A little hair on vertex and on upper mesopleura, otherwise nearly bare.

Clypeus nearly two and one-half times as broad as long, labrum fully one-half longer than clypeus, narrowed to less than one-half below, lower margin truncate; frontal groove complete, vertex about one-third broader than base of face; hind ocelli a little nearer eyes than to each other; third joint of antennae fully twice as long as broad.

Pronotum vertical in front, rounded into upper part, latter in middle hardly one-fifth of mesonotum, arcuate behind; propodeum, from side, sloping nearly evenly from base to hind border, about as

long as broad at base, narrowed toward tip a little; abdomen flattened especially toward tip; mid and hind tibiae with numerous little spines above and on outer side, indistinct below, inner spur about four-fifths of basitarsus.

In fore wings the marginal cell hardly half its length from wing-tip, fully as broad as submarginal cells; second submarginal cell only a little longer below than broad, narrowed one-third above, receiving the first recurrent vein before middle; third submarginal a little longer below than second, narrowed one-half above, outer side not as sloping as in many species, lower part curved, receiving the second recurrent vein (curved above middle) near middle; basal vein ends a little before transverse; in hind wings anal vein ends at forking of cubitus.

Length of fore wings 9 mm.

One male from Belem, Para, Brazil, 1 June (F. X. Williams). Type M.C.Z. no. 26822.

Notocyphus sigmoides spec. nov.

Male. Black, clypeus and labrum silvery, a short yellowish streak each side at lower orbit, in one specimen upper border of clypeus is pale; third segment of abdomen with a short, broad white spot each side in front (hidden if segment retracted), last segment above yellowish white; under side of basal joint of antennae pale; lower pleura, coxae, and outer side of mid and hind femora silvery. Fore wings rather evenly faintly blackish, veins black, hind wings but little paler.

Clypeus about twice as broad as long, labrum not longer, slightly tapering to the rounded tip; face very narrow below, antennae moderately long, third joint about equal basal, third plus fourth nearly equal vertex-width; hind ocelli a little nearer to eyes than to each other; pronotum moderately long in middle, about equal scutellum, arcuate behind; propodeum about as long as broad, from side slightly curved and sloping to tip, above on each side is an elongate area of silvery pubescence, enlarged around the spiracle and roughly forming a P.

Abdomen with fine whitish or grayish pubescence, the basal segment about as long as broad behind, beyond the second segment the abdomen is slightly compressed. Legs rather slender, inner spur of hind tibia about two-thirds of basitarsus; the inner branch of the bifid claw is sharp pointed; mid and hind tibiae with many small spines.

In fore wing the marginal cell is broader than the submarginals, but does not reach beyond them; second submarginal cell one and one-half times as long below as broad, base very oblique, apex much less so, receiving the first recurrent a little beyond middle; third submarginal a little longer below than second, very short above, about one-sixth to one-tenth of lower side, outer vein long, sloping then bent in a curve, receiving the second recurrent near middle; basal vein nearly interstitial with transverse, lower section bulges toward base; in hind wings the anal vein ends near or at forking of cubitus.

Length of fore wings 8 to 11 mm.

From Nova Teutonia, Santa Catharina, Brazil, January 2, 24, 25 (F. Plaumann). Type M.C.Z. no. 26590.

Notocyphus deceptus spec. nov.

In appearance closely similar to *N. sigmoides*, black body, slightly smoky wings, a white spot on each side of third segment, a small white spot at tip of abdomen; front tibia below, the tip, and the tarsus (except last joint) yellowish; the thorax, coxae, and propodeum sericeous; the first joint of antennae is not pale below; the face is not as much narrowed below as in *sigmoides*, and the clypeus, therefore broader, fully two and one-half times as broad as long, the labrum is also much broader at base and tapers more to the short tip; antennae shorter and less crenulate toward tip, third joint not twice as long as broad, second plus third plus fourth joints not nearly equal vertex-width. Pronotum a little shorter in middle, the hind margin being more deeply arcuate than in *sigmoides*; propodeum somewhat narrowed behind.

Abdomen plainly broader on second segment than in *sigmoides*; hind tibiae with a few small spines on inner side, none above, mid tibiae with more and smaller spines, some above; inner spur of hind tibiae about two-thirds of basitarsus.

In fore wings the marginal cell is similar to that of *sigmoides*, but not broader than the submarginals; the first recurrent vein ends beyond middle; the third submarginal is much broader at top than in *sigmoides*, being fully one-third of lower side, second recurrent (curved) ends near middle; the stigma is longer than that of *sigmoides*, plainly longer before origin of radius than beyond the basal vein.

Length of fore wings 7 mm.

One male from Nova Teutonia, Santa Catharina, Brazil, 8 February (Plaumann). Type M.C.Z. no. 26823.

Subfamily CERATOPALINAE

These have the labrum mostly exposed, but shorter than clypeus; body is largely bare, and venation similar to Notocyphus; there are only very small spines on mid and hind tibiae, the claws are cleft. The face is much narrowed below, and inner margin of eyes broadly emarginate, and the spiracle of propodeum is only about its length from base of propodeum; the hind legs are extremely long.

Ceratopales Schulz

1. Hind femora largely black; abdomen black, more or less marked with pale 2
   Hind femora largely rufous 3
2. Stigma yellowish; basal joint of antenna pale above; face densely, evenly, and rather coarsely punctate, punctate in ocellar area; scutellum plainly punctate ..... *taschenbergi*
   Stigma nearly black; basal joint of antenna black above; face not nearly so densely nor coarsely punctate, ocellar area raised and nearly smooth; hind femora with yellowish streak ..... *elsida*
3. Abdomen black, with some pale bands or spots, first segment with white mark each side ..... *azteca*
   Abdomen rufous, sometimes with pale or white bands 4
4. Pronotum on sides smooth, shining, scarcely punctate; mesonotum with a shallow furrow each side 5
   Pronotum plainly punctate, dull, not shining; mesonotum without lateral furrows 6
5. Black spot on clypeus; inner spur of mid tibia in female one-half of basitarsus ..... *isolde*
   No spot on clypeus, female with inner spur of mid tibia not one-half of basitarsus ..... *abdominalis*
6. All except first segment with apical pale band; hind tarsi dark only at tips of the joints ..... *brethesi*
   Pale bands on only fifth and sixth segments; hind tarsi wholly dark; wings slightly darkened ..... *bolivari*

Two of these species, isolde and bolivari, are described in a paper on new species from Northern South America.

Ceratopales brethesi spec. nov.

Head and thorax black; abdomen and legs reddish; in female usually a dark spot on labrum; clypeus and usual face mark white; antennae in female black except under side of first and second joints, in male black above, yellowish beneath except last few joints black;

hind margin of pronotum and basal humps white, also spot on scutellum and post-scutellum, and hind corners of propodeum also white; abdomen with narrow whitish apical band on all segments except the first, that on the last segment the broadest.

Coxae usually reddish, front coxae white in front, mid coxae white on outer side, hind coxae with white spot at tip above; front femora and tibia partly white, mid tibia white at base and tip above, hind tarsi dark at tips of joints. Pleura and propodeum with much silvery white tomentum. Wings hyaline, tip of fore wings a little darker, stigma yellowish, veins dark. Structure near *abdominalis*; vertex more finely punctate, mesonotum more coarsely punctate, and some trace of a median carina, but not interrupting puncturation, no lateral depressions; scutellum elevated and prominent. In female inner spur of mid tibia not one-half of basitarsus; in male the mid leg is much shorter than in female, first tarsal joint white, second, third, and fourth joints broader than long, and the fifth joint somewhat broadened in middle.

In fore wings the second submarginal cell twice as long below as broad, third below about as long as second, not one-half as long above as on lower side. Lateral ocelli fully their diameter from the much larger anterior ocellus, and about as near to eyes as to each other.

Length of fore wings, ♀ 10 mm.; ♂ 7.5 to 8.5 mm.

From Cordova, Argentine (W. M. Davis); Villa Rica, Paraguay, January and May (Schade); Urucum, Corumba, Brazil 28, 29 December (Cornell Exped.), and Tucuman, Argentine, 24 February (Cornell Exped.). Type M.C.Z. no. 26593, paratypes there and at Cornell Univ. This is probably the species referred to by Fox (p. 229) as Ceropales sp. from Corumba, as near *abdominalis* but with banded abdomen and more coarsely punctate thorax.

Ceratopales bolivari Banks

Described from Puerto Colombia, Colombia (Bequaert).

Ceratopales abdominalis Taschenberg

Male and female from Santa Cruz, Bolivia (Steinbach). In the male the mid tarsus has second joint fully twice as long as broad, third as long as broad, fourth a little shorter than broad, fifth moderately swollen. The pronotum is smooth and shining on the sides; the

lateral ocelli hardly diameter from anterior ocellus and nearer to each other than to eyes.

Smith in Brit. Mus. Cat. 206 says that the *Pompilus abdominalis* Fabricius is a Ceropales; if so Taschenberg's species must be renamed; however, the description would indicate some other genus.

Brethés (1913) puts *abdominalis* and *irregularis* Smith as synonyms of *Ceropales anomalipes* Shuckard. But several statements in his description do not agree; "pleura and metathorax with golden down," and a depression on each side of head would indicate that it is not a Ceropales. Taschenberg's description mentions no pale bands on the abdomen; an Argentine species with pale bands may have been identified as *abdominalis* by Brethés.

Ceratopales taschenbergi D. T.

Ceropales nigripes Taschenberg (preoccupied)

Specimens from Mendoza, 12 December (Jorgensen coll.), La Rioja (Giacomelli, Cornell Univ.); Cosquin, Sierra de Cordoba, 1–9 March (Cornell Univ. Exped.); Mendoza, 14 March (Cornell Exped.), all Argentina. The mid tarsus of the male is shortened, much as in other species; the vertex is just as densely punctate as the face; lateral ocelli a little nearer to each other than to eyes.

Ceratopales isolde Banks

Described from Muzo, Dept. Boyaca, Colombia (Bequaert).

Ceratopales azteca Cameron

Of this Central American species there is a pair from Sevilla, Magdalena, 15 February, 31 December, and another specimen from Vista Nieve, San Lorenzo Mt., 19 December, all Colombia. As noted by Cameron the labrum of female is black, in male yellowish. In the male the mid tarsus has the second joint nearly twice as long as broad, the third fully as long as broad, the fourth a little shorter, and the fifth but little broadened; the pronotum is shining on the sides; mesonotum with median carina behind, on each side a broad, shallow depression, here the punctures are numerous and large; inner spur of mid tibia of female is fully one-half of basitarsus; the stigma is yellowish, veins pale brown; flagellum black above and below in both sexes, except the third antennal joint is pale below.

Ceratopales elsida spec. nov.

Black, clypeus, labrum, lower face and up the orbits in usual manner whitish yellow; antennae brown above, yellowish below, except near tip; pronotum with a broad yellowish band across tip, in female almost wholly yellowish or rufous, the basal humps yellowish; the scutellum, postscutellum, and hind corners of propodeum white; abdomen with a rather broad band across tip of first segment, narrower apical bands on other segments, except the last which occupies one-half of the segment. All coxae black, front ones white beneath, mid and hind coxae with a whitish mark, rest of front legs yellowish, but basal part of femora above darkened, mid and hind femora and tibiae dark brown to black, the femora with a pale streak on lower outer side; tarsi pale, the tips of joints dark, and in hind tarsus the last joint dark. Wings hyaline, tips of fore wings plainly dark, stigma dark, almost black, veins brown.

Structure in general similar to *taschenbergi*, punctures of head and thorax above not as dense, front with more distinct groove than *taschenbergi*, the mesonotum not depressed each side; scutellum scarcely punctate; the propodeum and abdomen much as in that species. The ocellar region is distinctly elevated above vertex, polished, lateral ocelli over diameter from the anterior ocellus and plainly nearer to each other than to the eyes. In the female the inner spur of mid tibia is about one-third of basitarsus; in male the mid legs are shortened less than usual and the second, third, and fourth joints as long as broad.

In fore wings the second submarginal is not quite twice as long as broad.

Length of fore wing 6.5 mm.

From Vista Alegre, Rio Branco, Amazonas, 6 Sept. (Bequaert), and Santa Cruz, Bolivia (Steinbach). Type M.C.Z. no. 26596.

Irenangelus Schulz

This genus agrees in the shape of the face with Ceratopales, but differs in the crenulate antennae; the stigma is about half in marginal cell, and the claws are not cleft; however, it may be as near to Ceratopales as to any other genus. Several species have been described; I have seen but one.

Irenangelus reversus Smith (Agenia)

From Pomatumari, Potaro River, British Guiana, 28 June, (Cornell Univ. coll.).

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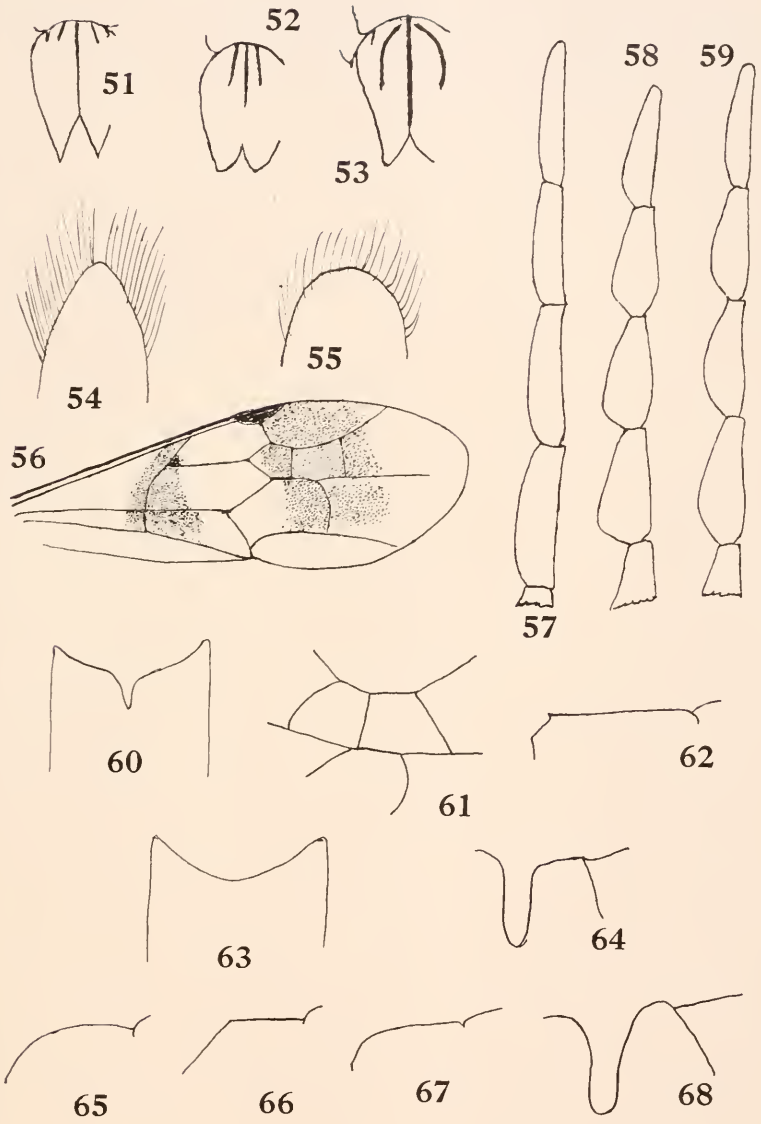
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MIOCENE RODENTS FROM FLORIDA

BY ALBERT E. WOOD

WITH ONE PLATE

CAMBRIDGE, MASS., U. S. A.
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No. 3 — *Miocene Rodents From Florida*

BY ALBERT E. WOOD

At various times since 1932, a few additional rodent specimens have been found in material from the Middle Miocene Hawthorn Formation, mostly from the Thomas Farm locality, Gilchrist County, Florida. A sufficient number have now accumulated to warrant a brief description. I wish to express my appreciation to the Florida State Geological Survey for lending me the mylagaulid specimen, and to Dr. A. S. Romer and the Museum of Comparative Zoölogy for lending me most of the other material discussed. The remaining material was collected by me in 1935 while Cutting Traveling Fellow in Columbia University. This study was aided by a grant from the Marsh Fund of the National Academy of Sciences. Figures 5 and 6 were drawn by Dr. Florence Dowden Wood.

PROHETEROMYS FLORIDANUS Wood, 1932

Three additional slightly worn molars of this form have come to light, two lowers and one upper (Figs. 1–3). These teeth are much less worn than the molar of the holotype, and require a slight revision of the specific diagnosis (Wood, 1935, p. 166). The two lower molars show a very clear but primitive Y-pattern, there being a deep valley between the protoconid and the protostylid (for cusp terminology, see Wood and Wilson, 1936). The identification of these two teeth as M/1 and M/2 respectively is tentative — the correct identification may be the other way around. Both of these teeth clearly show a spur from the hypoconid extending across, or partly across, the central valley, to the protoconid. This is the beginning of the H-pattern, a basic development in the Heteromyinae, to which subfamily this form belongs.

These specimens demonstrate that the tooth identified by Wood as M 3/ of *P. magnus* (1932, p. 48) and later as M/3 of *P. magnus* (1935, p. 169) almost certainly is referable to *P. floridanus*, and is more likely M/2 than any other tooth. It appears in every way identical with the tooth here considered to be M/2.

M/1, as here identified, has a long, narrow hypostylid extending as a blade the whole width of the metalophid (Fig. 1). The protostylid is similar in shape, but is longer and is connected via the anterior cingulum to the protoconid and metaconid. The three unite at about

the center of the anterior face of the tooth. There is no posterior cingulum and the spur from the hypoconid toward the protoconid is short.

The other lower molar is believed to be M/2 because the hypostylid is only a small, rounded conule. In general, the hypostylids in heteromyids become progressively smaller from M/1 to M/3. It also differs from M/1 in having a longer protostylid and a tiny cuspule in the middle of the posterior side of the tooth, representing the posterior cingulum.

The upper tooth (Fig. 3) is tentatively identified as LM 1/, though it may be LM 2/. It is very similar to the tooth previously described as RM 1/, showing no significant differences.

	RM/1 AEW 9244b	RM/2 MCZ 3648	LM 1/ AEW 9244a
antero-posterior	0.78 mm.	0.88 mm.	0.84 mm.
width, anterior loph	0.94	0.92	1.13
width, posterior loph	0.88	0.91	1.07

In most heteromyids, the antero-posterior diameter of M/1 is greater than that of M/2, but in the Heteromyinae there appears to be no constant relationship between the diameters of these two teeth. As in general among the heteromyids, the transverse diameter of the upper molars is greater than that of the lowers.

Proheteromys magnus Wood, 1932

A single additional molar of this species, M. C. Z. 3649, LM/2 (Fig. 4) adds little to the knowledge of this form, being considerably more worn than the specimen previously described (Wood, 1932, Fig. 27). It shows, however, that the hypostylid is rapidly lost with wear, and that the posterior cingulum is the next element of the pattern to disappear.

	LM/2, M. C. Z. 3649
antero-posterior	1.52 mm.
width metalophid	1.53
width hypolophid	1.48

This tooth is about ten percent smaller than Fla. St. Geol. Surv. No. V-5333, only part of the difference being due to wear.

Mesogaulus new species

The most interesting new material is an isolated RP/4 of a mylagaulid, from the Fuller's earth mine at Midway, Florida (Fla. St. Geol. Surv. No. V–5422, Figs. 5–7). This tooth appears to be referable to *Mesogaulus* Cook and Gregory, previously known from the Miocene of the Great Plains, and is perhaps closest to *M. praecursor* of the Lower Miocene of Nebraska. The specimen is fairly high crowned, and the roots are not strongly developed. There is a distinct groove down the lingual side, marking the boundary between the trigonid and talonid. The crown pattern (Figs. 6–7) shows six lakes. These do not show the marked transverse compression and antero-posterior elongation seen in most mylagaulids (including *Mesogaulus praecursor*). In part this may be due to the relatively unworn condition of the present tooth, but it seems to represent a Middle Miocene retention in the Florida cul-de-sac of a primitive mylagaulid condition which had already been lost in the western forms, which were presumably nearer the center of evolution of the family. The six lakes of the Florida tooth can be homologized with the five shown by Cook and Gregory for *Mesogaulus laevis* (op. cit., Fig. 1), by assuming that the two anterior fossettids represent the anterofossettid of the western forms. The Florida *Mesogaulus* is certainly among the most primitive members of the family. It seems best, however, not to name it until it can be considered in connection with a review of the entire family.

Height of crown by protofossettid	8.8 mm.
antero-posterior diameter, base of crown	7.5
antero-posterior diameter, worn surface	4.9

Cricetid indet.

Parts of five humeri are preserved in the M. C. Z. material. These are all of the same size group, and were at first tentatively referred to *P. floridanus*. However, they differ from the humeri of all heteromyids with which they have been compared, and particularly from those of *Cupidinimus nebraskensis* from the Lower Pliocene of Nebraska (Wood, 1935, Fig. 57) in important features, which are points of resemblance to the Cricetidae. The deltoid crest is short and trapezoidal in shape, with subequal distal and proximal slopes. Instead of rising to a point as in heteromyids, there is a fairly long ridge of uniform height (Fig. 8). A supracondylar fenestra is present, not known in the heteromyids but present in the cricetids. While no complete bone is

present, it is possible to estimate the length of the humerus in this form as about 10 mm., which indicates an animal about the size of *Peromyscus*.

A considerable number of incisors are associated with the material, particularly in the collections of the Museum of Comparative Zoölogy. There are over fifty such incisor fragments, which fall into three categories. All of them have pigmented enamel, now usually dark brown or black. They are all narrow, compressed, with a rounded anterior face, and a limited extension of enamel onto both mesial and lateral surfaces. However, in some, the enamel extends over about a quarter of the lateral surface as in cricetids, and in others over about two-fifths, as in heteromyids.

Two incisors are separable from the others because of their larger size. They show the enamel extending well around onto the lateral surface, as in heteromyids, and may be referred to *Prohcteromys magnus*.

Of the other incisors, about half appear also to be those of heteromyids. These teeth are a trifle larger than those of *Cupidinimus nebraskensis*, and are believed to have belonged to *P. floridanus*. Since the cheek teeth of the latter form are somewhat smaller than those of *Cupidinimus*, this would indicate that the Florida form had proportionately heavier incisors than do most heteromyids.

The last group of incisors appear to be cricetid, and are probably associated with the humeri discussed above and the other limb bones mentioned below.

The M. C. Z. material includes parts of seven femora, five of which are mere fragments. It appears, however, that they can be separated into two groups. In one, the third trochanter begins distad of the lesser trochanter, and the highest point of the third trochanter is some distance farther distad. This makes the shaft fairly broad for some distance distad of the lesser trochanter. The neck is nearly in the plane of the long and transverse axes of the femur. These femora appear to be heteromyid. In the second group, the third trochanter is farther proximad and the shaft is more slender. The neck is at an angle to the plane of the long and transverse axes of the femur. The only nearly complete femur of the series (ca. 14.5 mm. long) is in this group. It appears very similar, both in size and structural features, to that of *Peromyscus*, and is considered to be cricetid.

Of four small calcanea in the M. C. Z. collection, two appear to be heteromyid in that there is a marked depression on the dorsal surface, just behind and below the fibular keel, as in *Cupidinimus*. There is a

slight difference in size between these two specimens, and it is possible that one may belong to *P. floridanus* and the other to *P. magnus*. The other two calcanea do not show this depression, in which they agree with *Peromyscus*, and are hence considered to be cricetid.

In conclusion, this small collection, though by no means as complete for any form as might be desired, adds appreciably to our knowledge of the Middle Miocene rodent fauna of Florida. Besides additional material of the two species of *Proheteromys*, hitherto the only rodents described from the Florida Miocene, there is unmistakable evidence of cricetids in the fauna, as would naturally be expected, as well as of a primitive mylagaulid, the first member of the family to be found east of the Great Plains. The previous absence of the Mylagaulidae in collections from eastern North America is not particularly phenomenal, in view of the extreme rarity of smaller Tertiary mammal fossils east of the Mississippi.

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PLATE

PLATE

Fig. 1. *Proheteromys floridanus.* AEW No. 9244b, RM /1, x 10

Fig. 2. *P. floridanus.* MCZ No. 3648, RM /2, x 10

Fig 3. *P. floridanus.* AEW No. 9244a, LM 1/, x 10

Fig. 4. *P. magnus.* MCZ No. 3649, L M /2, x 10. Anterior end of tooth to the right.

Fig. 5. *Mesogaulus* n. sp. Fla. St. Geol. Surv. No. V–5422, RP /4, lingual view, x 3 1/3

Fig. 6. *Mesogaulus* n. sp. Fla. St. Geol. Surv. No. V-5422, RP /4, crown view, x 3 1/3

Fig. 7. *Mesogaulus* n. sp. Identification of fossettids.

1 = protofossettid
2 = anterofossettid
3 = mesofossettid
4 = metafossettid
5 = hypofossettid

Fig. 8. Cricetid, indet., MCZ not numbered, x 10/3

8a. Lateral view, proximal end right humerus.

8b Anterior view, distal end right humerus.

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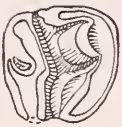

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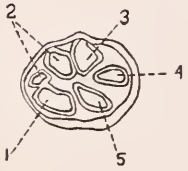

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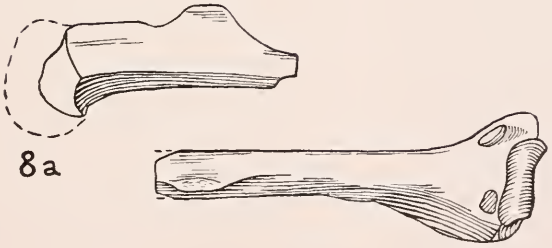

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ADDITIONS TO THE MIOCENE FAUNA OF NORTH FLORIDA

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PRINTED FOR THE MUSEUM
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OF THE

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No. 4—*Additions to the Miocene Fauna of North Florida*

By Theodore E. White

The late Dr. Thomas Barbour always maintained a keen interest in the excavations on the Thomas Farm in North Florida. With the aid of the two men who served us so well in the past, he continued the excavations during the period of hostilities. The material accumulated during this period, and that which the writer collected in the winter of 1946 has added six genera and seven species to the fauna of this deposit, as well as increasing our knowledge of previously described forms. Three of the genera were previously known only from the Upper John Day-Lower Rosebed and two from the Middle and Upper Miocene deposits of the Plains. Consequently the correlation of these deposits on the basis of the fauna is still in the same paradoxical position that it was.

The number of forms known from fragments too imperfect for proper diagnosis remains distressingly large. To date the list is: didelphids, an imperfect lower molar and a toothless lower jaw; insectivores, a single lower molar; rodents, incisors, cheekteeth and footbones; mustelids, isolated teeth and toothless lower jaws.

Family MUSTELIDAE

Aelurocyon spissidens spec. nov.

Type. M. C. Z. 4246 (Fig. 1, A and B), portion of left mandible with P_4 and M_1 and the alveoli for P_{2-3} and M_2.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. A small species, about one-third smaller than *A. brevifacies* Peterson; teeth higher crowned; premolars crowded together, overlapping, and set obliquely in the jaw with the anterior end slightly lateral to the posterior; fourth premolar with a small but well defined anterior tubercle, posterior tubercle and accessory cusp well developed; carnassial with small tubercle between protoconid and hypoconid; second molar two-rooted.

Measurements (in millimeters)

	spissidens		*brevifacies**	
	Length	Width	Length	Width
P_2 to M_2 (alveolar)	48			
P_4	10	5	17	10
M_1	17	7	21	10
Depth of jaw at P_3	19		35	
" " " " M_2	21		37	

* Taken from Peterson, O.A., 1906 C.

Discussion. There appears to be a vestige of the metaconid represented by a minute tubercle on the postero-medial side of the protoconid. There is a low narrow cingulum on the medial side of the heel of the carnassial and the hypoconid is placed more laterally than medially. There was a small premolar crowded in between the canine and the second premolar. The posterior portion of the mandible was broken away and the presence or absence of a third molar could not be determined. There are two mental foramina of nearly equal size.

Oligobunis floridanus spec. nov.

Type. M. C. Z. 4064 (Fig. 1, C and D), left mandible with P_3 to M_1.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. Slightly larger than *O. crassivultus* Cope; second premolar with single bilobed root; third premolar with distinct heel and minute accessory cusp; fourth premolar with distinct heel and accessory cusp; carnassial narrows abruptly posterior to the protoconid, shear very oblique, metaconid strong and as high as the paraconid, width of heel equal to two-thirds the width at the metaconid.

Measurements (in millimeters)

	Length	Width
P_3 to M_1	36	
P_3	8	4.0
P_4	11	5.5
M_1	17	8.0

Discussion. Although the jaw was badly crushed, it is believed that approximately the correct curvature was obtained in the restoration.

The teeth show little wear, except the carnassial, which exhibits the characteristic mustelid wear. This specimen does not permit us to add anything to the discussions of this genus given by Matthew (1907 A), Thorpe (1921 C), and Loomis (1932 A).

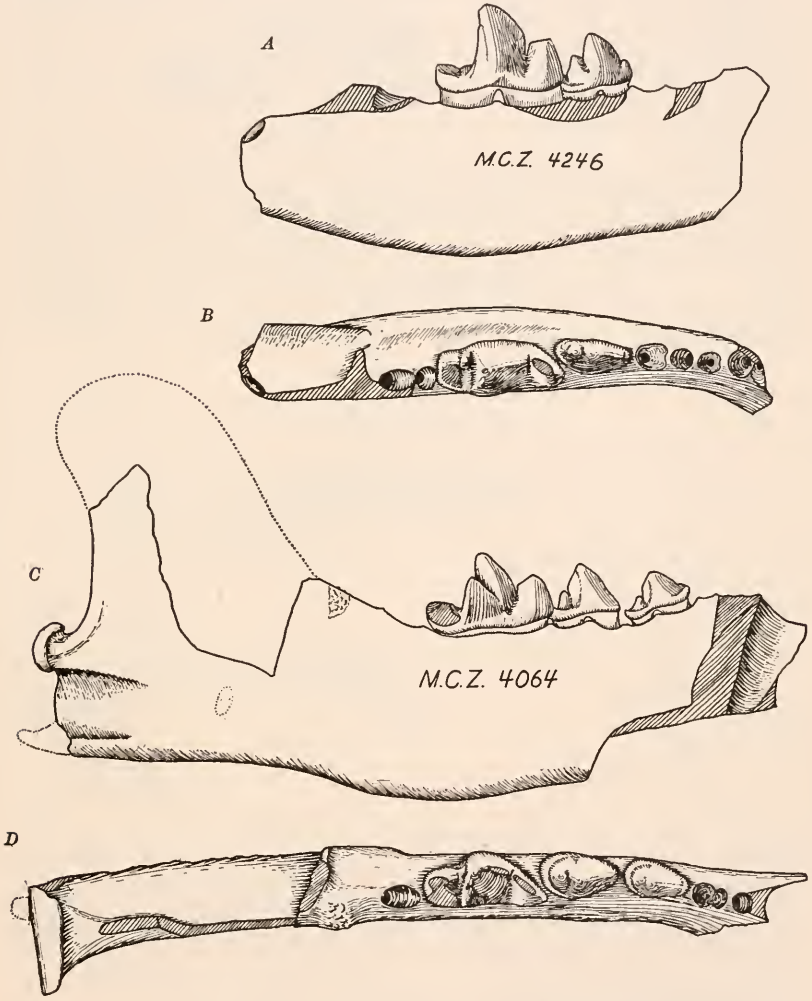

Fig. 1. A and B, *Aelurocyon spissidens* sp. nov., type, medial and occlusal views. x 1. C and D, *Oligobunis floridanus* sp. nov., type, medial and occlusal views. x 1.

Family CANIDAE

Paractis bathygenus spec. nov.

Type. M. C. Z. 3931 (Fig. 2, B and C), portion of left mandible with P_4 to M_2.

Referred Specimen. M. C. Z. 3930 (Fig. 2, A), a partial palate with P^4 to M^2 of both sides.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. As large as *Mesocyon coryphaeus*; mandible deep and massive, depth at the anterior end of the first molar nearly equal to the combined length of the first and second molars; fourth premolar with minute tubercle and accessory cusp; heel of carnassial with large hypoconid and small entoconid; second molar seven-ninths as broad as long, protoconid and metaconid opposite and subequal, paraconid represented by a minute tubercle, hypoconid small but distinct.

Measurements (in millimeters)

M. C. Z. 3931

Depth of mandible between P_4 and M_1	22
" " " " M_2 and M_3	25

	Length	Width
P_4 to M_2	34	
P_4	10	4.5
M_1	15	7.0
M_2	9	7.0

M. C. Z. 3930

P^4 to M^2	27	
P^4	14	8.5
M^1	10	12.0
M^2	5	8.0

Discussion. The basis for referring the upper dentition to this species is its excellent occlusion with the type. The upper dentition bears a close resemblance to that of *Mesocyon* but differs in the following respects: On the fourth premolar the deuterocone is better developed and is slightly constricted off from the paracone. On the labial side the enamel does not curve so sharply downward, posteriorly. On the first molar the external cingulum is less pronounced and the internal cingulum forms a low, broad ridge which is slightly crenulated on the labial side. The protocone is not so well developed. The reëntrant

angle on the posterior side of the tooth, medial to the protocone, is more pronounced. The second molar is less well developed and the reëntrant angle on the posterior side of the tooth is more pronounced.

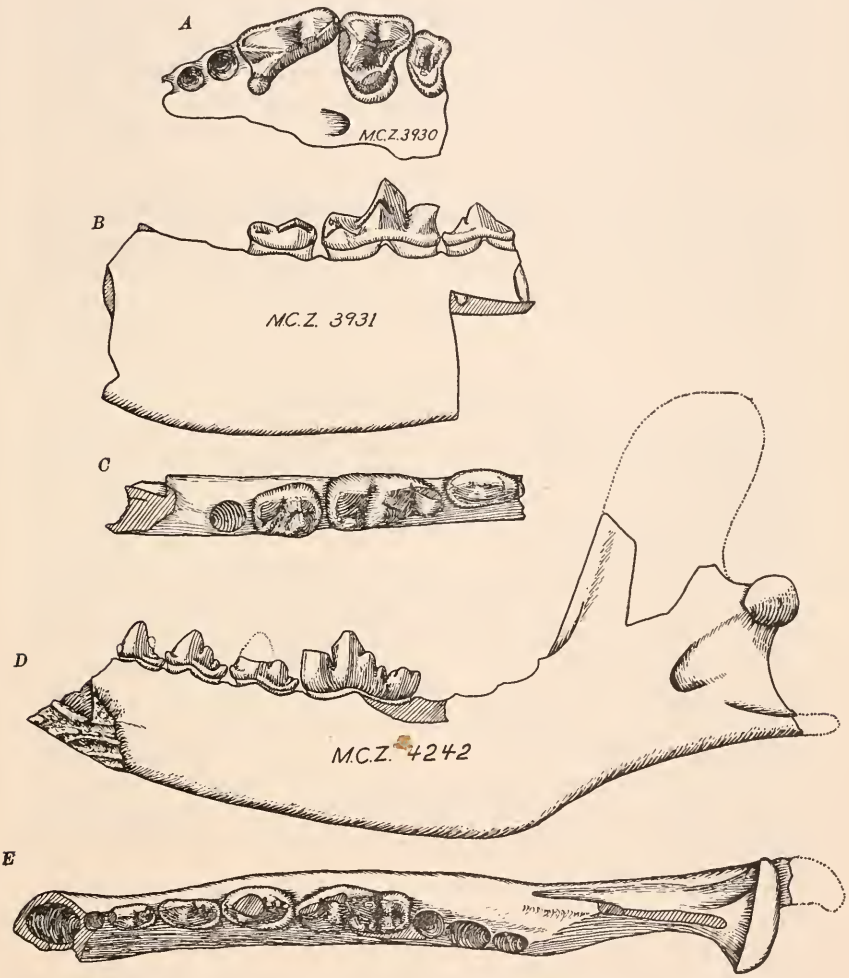

Fig. 2. A, *Parictis bathygenus* sp. nov., referred specimen, occlusal view. x 1. B and C, *Parictis bathygenus* sp. nov., type, medial and occlusal views. x 1. D and E, *Nothocyon insularis* White, medial and occlusal views. x 1.

The type of *Mesocyon hortulirosae* Schlaikjer and a cast of the type of *M. drummondanus* Douglass were used for comparison.

A comparison of the type with a specimen of *Amphicynodon rossignoli* (Filhol) shows, as Scott & Jepsen (1936) pointed out, that the two genera are, indeed, closely related. However, the fourth premolar of this species does not have the well developed accessory cusp found on *P. primaevus* Scott, *P. dakotensis* Clark, and *A. rossignoli* (Filhol). In addition to the above resemblances, the characters of the lower teeth and the massiveness of the lower jaw appear to be prophetic of *Ursavus* Schlosser.

On the basis of this specimen and other fragmentary material in the Museum of Comparative Zoölogy, it seems highly probable that more than one genus was living in North America during the Oligocene and Miocene. However, a division, based on the imperfect and limited material now available, is entirely unwarranted.

Nothocyon insularis White

Bull. Mus. Comp. Zoöl., **92**, No. 1, p. 7, Pl. 1, fig. 3, 1942.

Referred Specimen. M. C. Z. 4242 (Fig. 2, D and E), right mandible with P_2 to M_1.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Discussion. The specimen is referred to this species on the basis of occlusion with the type. Although there is little difference in the alveolar length (63 to 67 mm.) between this specimen and a referred specimen of *Tomarctus canavus* Simpson, it is much lighter in construction and more slender throughout. The condyle of the jaw is shorter, smaller, and set at an oblique angle with the mandible, indicating a broad skull for this form. The individual teeth are smaller and shorter crowned, but the cusps agree in position with those of *T. canavus*. As in *Nothocyon vulpinus coloradoënsis* Thorpe (1922 E) the heel of the carnassial shows the ridge between the hypoconid and entoconid that is characteristic of *Tomarctus*.

Measurements (in millimeters)

	N. insularis	*T. canavus*
M. C. Z. number	4242	3628
Alveolar length (exclusive of canine)	63	67

	N. insularis		*T. canavus*	
	Length	Height	Length	Height
P_2	8	5	7.5	5
P_3	8.5	5.5	8.5	6
P_4	9	—	10	7.5
M_1	16	8.5	17	10
Depth of jaw at P_3	15		18	
" " " " M_1	17		21	

AELURODON JOHNHENRYI spec. nov.

Type. M. C. Z. 4059 (Fig. 3, B and C), right mandible with C, P_2 to M_2.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. As large as *A. haydeni* (Leidy) but with a relatively longer jaw; second and third premolars elongate antero-posteriorly and with relatively low principal cusp; second, third, and fourth premolars widest a little posterior to their midlength and with posterior tubercle and accessory cusp; third and fourth premolars with minute anterior tubercle; carnassial of the same size and proportions as *A. haydeni*, hypoconid well developed, entoconid small; second molar with protoconid and metaconid opposite and subequal, protoconid larger, hypoconid well developed and placed medially on the heel, no entoconid.

Measurements (in millimeters)

C to condyle	203	
Depth of jaw at M_2	42	
	Length	Width
P_2	12	6
P_3	14	7
P_4	18	10
M_1	34	14
M_2	21	15

Discussion. Although the anterior premolars of this form are very different from those of other species of *Aelurodon*, it agrees so well with the characters of that genus, as set forth by Vanderhoof and Gregory (Univ. Calif. Publ., Bull. Dept. Geol. Sci., **25**, No. 3, pp. 143-164, 1940), that a separate genus seems unwarranted. These authors derive *Aelurodon* from *Tomarctus* through an as yet unknown species. The second and third premolars give this species an isolated position

in the genus *Aelurodon*, but it exhibits a number of characters which have not departed far from the condition found in *Tomarctus*. These characters are: the nearly straight tooth line, the general form of the premolars, the unreduced metaconid on the carnassial, the unreduced second molar, and the general form of the mandible.

Family PROTOCERATIDAE

Synthetoceras (Prosynthetoceras) douglasi spec. nov.

Type. M. C. Z. 4065 (Fig. 3, A), a badly crushed palate with P^3 to M^3 of both sides.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. Smaller than *S. francisi*; anterior external style on third and fourth premolars less well developed; first and second molars as in *francisi*; external and internal mesostyles on the third molar as in *Protoceras*; anterior and posterior cinguli on the second molar and anterior cingulum on the third molar.

Measurements (in millimeters)

P^3 to M^3	66	
	Length	Width
P^3	9	6
P^4	9	9
M^1	14	13
M^2	17	15
M^3	17	16

Discussion. Unfortunately the bone in this specimen was very poorly preserved and it tended to disintegrate on exposure. It was saved only with great difficulty. The portions of the skull which would have borne the horns are missing. The internal nares are large and anterior in position. Their anterior border is opposite the posterior crescent on the second molar. It is impossible to determine the presence or absence of a second premolar. The third premolar is similar to that of *S. francisi* except that the anterior external style is not so well developed. The fourth premolar is as broad as long while in *francisi* it is broader than long. The first and second molars agree with those of *francisi* except that the posterior cingulum on the second molar

is better developed in this form. The third molar resembles that of *Protoceras* more than it does that of *S. francisi*. In general, this form is less advanced toward the peculiar specializations of the genotype than the other members of the genus.

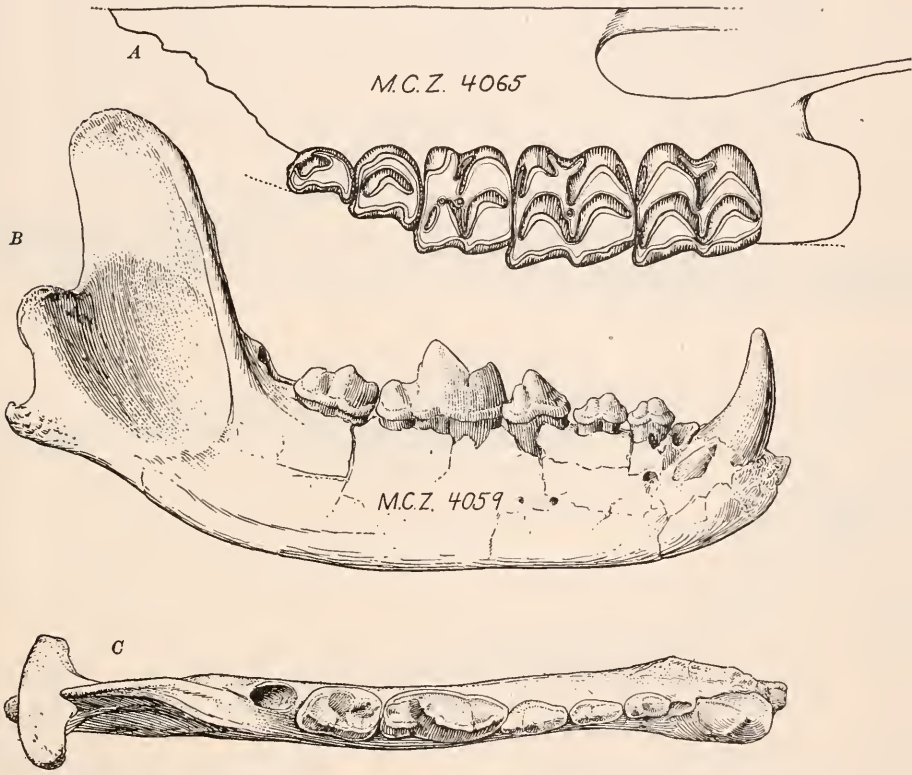

Fig. 3. A, *Synthetoceras douglasi* sp. nov., type, occlusal view. x 1. B and C, *Aelurodon johnhenryi* sp. nov., type, lateral and occlusal views. x ½.

Family HYPERTRAGULIDAE

Floridatragulus barbouri spec. nov.

Type. M. C. Z. 4086 (Fig. 4) a left mandible with C, P_2 to M_3.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Diagnosis. Smaller than *F. dolichantherius* and with a much shorter diastema between the second and third premolars.

Measurements (in millimeters)

		barbouri	*dolichantherius*
Diastema,	C to P_1	29	41
"	P_1 to P_2	38	43
"	P_2 to P_3	10	32
Length,	P_3 to M_3	69	75
"	M_1 to M_3	49	55

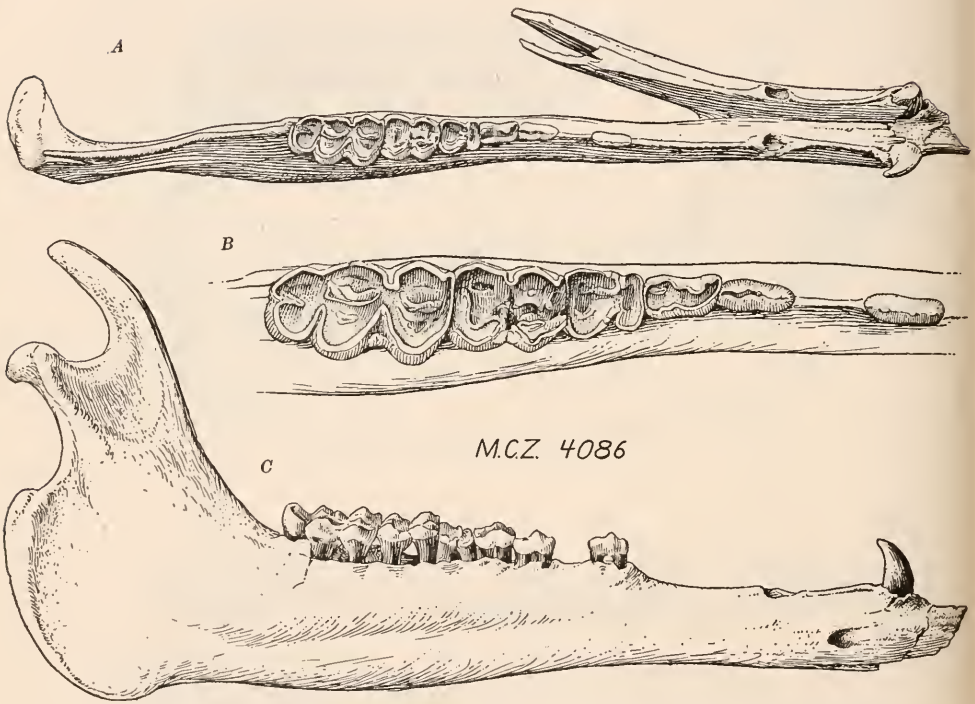

Fig. 4. *Floridatragulus barbouri* sp. nov., type, occlusal and lateral views. A and C, x ½, B, x 1.

	Length	Width	Length	Width
P_2	10.5	3		
P_3	10.5	4		
P_4	9	5		
M_1	10	9	13	9
M_2	15	11	16	11
M_3	24	12	26	12

Discussion. Since the canine and the second premolar do not show any wear, it is probable that they did not occlude with any of the upper teeth. The canine is short, compressed, and strongly recurved. The premolars resemble those of *Leptomeryx* in that the anterior and posterior cusps are nearly as high as the central. The second premolar is low, compressed, and has a rudimentary antero-internal fold. The third premolar has a stronger antero-internal fold and a rudimentary postero-internal fold. The fourth premolar has well developed antero-internal and postero-internal folds. The molars resemble those of *Leptomeryx* in that the external style between the crescents is rudimentary.

As yet no skeletal material certainly referable to this group of hypertragulids has been found.

Family TAYASSUIDAE

Floridachoerus olseni White

Proc. New Eng. Zoöl. Club, **18**, p. 93, Pl. 14, Fig. 4, 1941.

Referred Specimen. M. C. Z. 4290 (Fig. 5, C), a palate with left P^2 to M^3 and right M^1 to M^3.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Revised Generic Diagnosis. I^{1+}, C, P^4, M^3, no diastema behind canine; first premolar two-rooted and placed medial to the posterior portion of the canine; second premolar three-rooted with a single principal cusp, a strong ridge between the cusp and the internal cingulum, external and internal cinguli well developed; third premolar similar to the second but larger and with the external cingulum less well developed; the fourth premolar with two principal cusps and with a well developed cingulum running all the way around the tooth; strong ridges run antero-laterally and postero-laterally from the medial cusp so that the cusp sits at the apex of a well defined crescent; molars four-cusped and with moderately well developed anterior and posterior cinguli; third molar with small accessory cusps placed medially on the anterior and posterior borders.

Measurements (in millimeters)

I^3 to canine	13	
P^1 to M^3	96	
P^1 to P^4	48	
	Length	Width
P^1 (alveolus)	9	—
P^2	10.5	10
P^3	13	14.5
P^4	12	17

The molars were damaged so that reliable measurements could not be taken.

HYPERTRAGULOIDEA, *incertae sedis.*

Nothokemas gen. nov.

Genotype. Paratylopus grandis White; Proc. New Eng. Zool. Club, **18**, p. 33, Pl. 5, 1940.

Diagnosis. A large hornless artiodactyl with unreduced nasals; lacrymal vacuity as large as the orbit; rostrum high, narrow, and moderately elongate; postorbital bar complete; teeth slightly more hypsodont than *Syndyoceras*; premolars and molars similar to those of *Protoceras*; internal crescents of the upper molars and the external crescents of the lower molars separate to the base of the tooth; mesostyle of the molars rudimentary; heel of third lower molar single lobed; orbit and internal nares posterior to third upper molar; cuboid and navicular probably separate.

Referred Material. M. C. Z. No. 4329 (Fig. 6) a crushed skull with occiput and tip of the rostrum missing; No. 4322 (Fig. 5 A) right maxilla with P^2 to M^3; No. 4325 (Fig. 5 B and 6 C), left mandible with M_1 to M_3; No. 4323, left mandible with P_3 to M_3; No. 4324 (Fig. 5 B), left mandible with P_2 to P_4; No. 4326, left mandible with Dp_{3-4} M_{1-2} No. 4328 left maxilla with $Dp^{2-4}M^1$.

Horizon and Locality. L. Miocene, L. Arikareean, Thomas Farm, Gilchrist Co., Florida.

Discussion. These specimens supplement each other, so that it is possible to get a reasonably reliable concept of the skull and dentition of this genus. The skull (Fig. 6) is elongate with a moderately high, narrow rostrum. The orbit appears to have been nearly circular and completely closed behind. It is located nearly one-half of its diameter posterior to the last molar. The lacrymal vacuity is quadrangular in

outline and is contained entirely within the maxilla. The superior and postero-inferior edges are thickened. Its diameter nearly equals that of the orbit from which it is separated by a distance equal to two-thirds of its diameter. The anterior tip of the nasals has been lost but the part preserved, from a point opposite the first premolar, shows no evidence of emargination. They are long and narrow and are suturally united with the maxillaries. The profile appears to have been nearly straight.

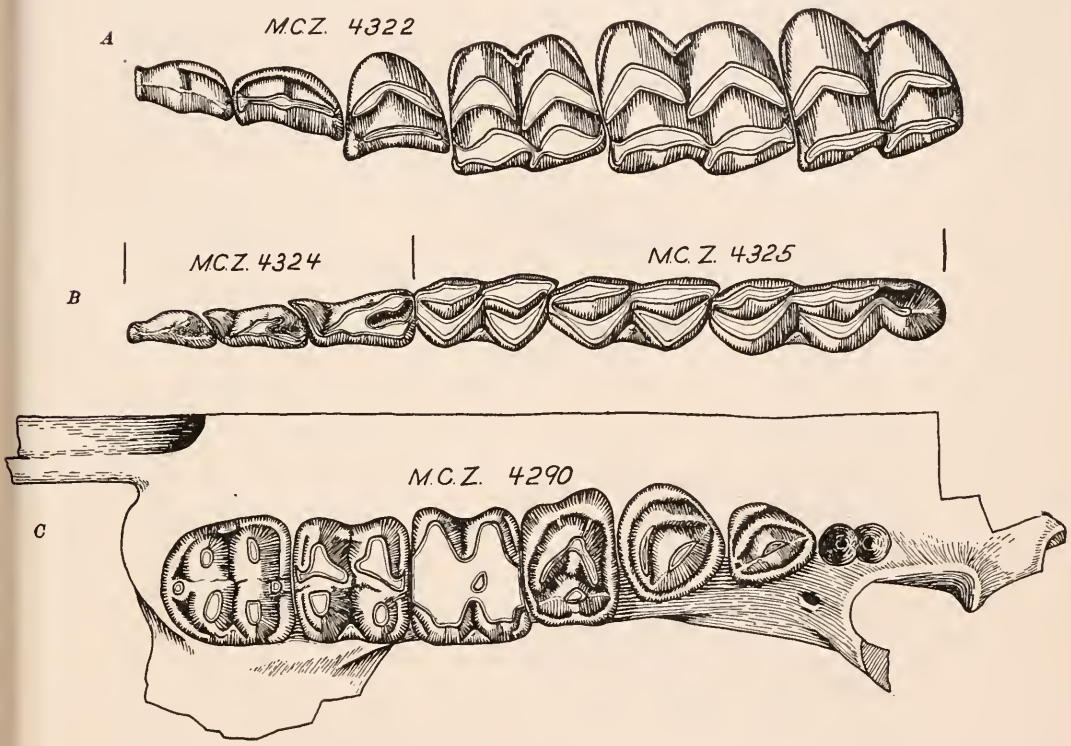

Fig. 5. A and B, *Nothokemas grandis* (White), occlusal views of upper (A) and lower (B) dentitions. x 1. C, *Floridachoerus olseni* White, occlusal view of upper dentition. The molars have been restored from the type and individual teeth. x 1.

The palate is very narrow anteriorly and wide posteriorly with the internal nares opening posterior to the last molar. The first premolar is represented by a very small oval alveolus which is separated from the

other teeth by a diastema on either side. The second premolar (Fig. 5, A) is two-rooted, compressed, elongated and with the cusps poorly developed. The third premolar is three-rooted with a strong internal cingulum. The outer crescent is similar to that of the second premolar

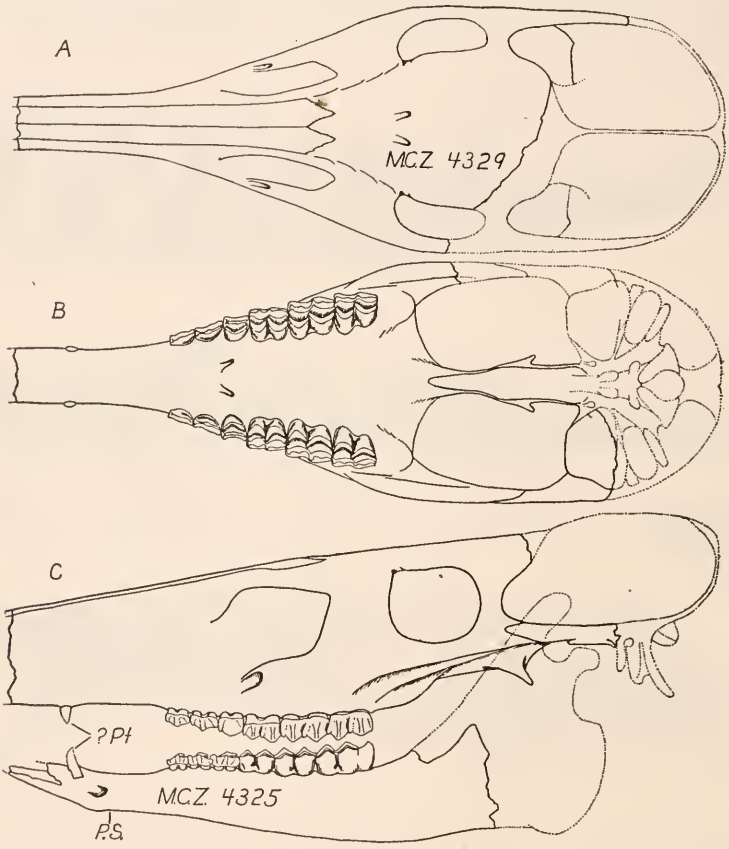

Fig. 6. *Nothokemas grandis* (White), restoration of the skull and lower jaw, (A) dorsal, (B) palatal views of the skull, (C) lateral view of skull and lower jaw. P.S. - posterior border of the symphysis. x ¼.

but with the cusps better developed. The fourth premolar and the molars differ from those of *Protoceras* principally in size and height of crown.

The form of the lower jaw (Fig. 6, C) is best shown by that of a young adult (No. 4325) in which the incisor region is badly damaged and the posterior end missing. The general form is of the cervoid type with a very long symphysis, which is incompletely fused in the old individuals. The posterior border of the symphysis is located about halfway between the first and second premolars and just behind the mental foramen. The anterior portion of the jaw is too poorly preserved to show any details of the sockets for the incisors or the canine. The second premolar (Fig. 5, B), is compressed, with a rudimentary antero-internal fold and a postero-internal fold which extends about halfway to the posterior end of the tooth. The third premolar has well developed antero-internal and postero-internal folds. In neither the second nor the third premolars would the postero-internal folds enclose a lake of enamel with wear. The fourth premolar has strong antero-internal and postero-internal folds. Near its posterior end, the latter is swollen into a cusp which constricts the enclosed enamel lake at about the middle of its length. This cusp appears to be homologous with the postero-internal cusp of *Leptomeryx*. The first and second molars differ from those of *Protoceras* only in the larger size and the greater height of crown. The third molar differs from all other members of this group in that the heel has only a single lobe, the outer. The inner lobe is represented by a short extension of the posterior crescent and is separated from the outer lobe to the base of the tooth. From the material at hand, it is impossible to be certain whether this is a rudimentary condition, which has persisted, or that the inner lobe has become reduced. This result could have been achieved by increasing the height of the crowns of the teeth of an Eocene hypertragulid such as *Leptotragulus*.

The artiodactyl tarsal material from this deposit was reviewed in the hope that some information relative to the affinities of the known forms could be obtained. Forms with fused cuboid and navicular are limited to two size groups. These are, with reasonable certainty, referable to *Parablastomeryx* and *Machaeromeryx*. The remaining separate cuboids can be divided into eight size groups. The animals thus represented have a size range from smaller than *Parablastomeryx* to nearly as large as *Cervus canadensis*. But the two smallest groups of cuboids are not large enough to belong to animals with any of the known dentitions. None of the groups is, with any reasonable degree of certainty, referable to *Floridachoerus*. In view of the relative scarcity of the remains of that form, it is entirely possible that its tarsus is not represented. One of the groups of cuboids appears to be referable to

	Archaeomeryx	Leptotragulus	Hypertragulu
Deuterocone on P_2	absent	small	absent
" " P_3	well developed	well developed	small
Internal cingulum on P_3	weak anterior and posterior	moderate, anterior and posterior	strong, anterior posterior
Inner crescent on P_4	primitive	cervoid	primitive
Inner crescents on upper molars	separate	separate to base of tooth	anterior separate, erior confluent small amount of
Anterior and posterior cusps on P_2	nearly as high as central	?	absent
Ditto on P_3	nearly as high as central	?	anterior absent, terior low
Ditto on P_4	nearly as high as central	low	low
Postero-internal fold on P_2	absent	?	absent
Ditto on P_3	absent	?	absent
Ditto on P_4	rudimentary	present	rudimentary
Antero-internal	absent	?	absent
Ditto on P_3	present	?	absent
Ditto on P_4	present	present	present
Outer crescents on on lower molars	separate	separate	anterior separate terior confluent inner with sma amount of wear.
Heel of M_3	single	single	double
Orbit	closed	open posteriorly	open posteriorly
Nasals	normal	normal	normal
Lacrymal vacuity	absent	absent	small, between fr nasal, lacrymal maxilla
Cuboid and navicular	fused	probably separate	fused

anotragulus	Heteromeryx	Leptomeryx	Nothokemas
ent	small	well developed	well developed
ll	well developed	well developed	absent
erior only	weak anterior, strong posterior	strong anterior and posterior	strong, complete
nitive	cervoid	cervoid	cervoid
luent with inner small amount of r	separate to base of tooth	separate to base of tooth	separate to base of tooth
ent	?	nearly as high as central	nearly as high as central
ent	?	nearly as high as central	nearly as high as central
ly as high as ral	?	nearly as high as central	nearly as high as central
nt	?	absent	short
nt	?	rudimentary	well developed
nplete	?	complete	complete
nt	?	present	present
nt	?	present	present
ent	?	present	present
luent with inner small amount of	?	separate to base of tooth	separate to base of tooth
ole	?	double	single
posteriorly	closed	closed	closed
nal	somewhat reduced	normal	normal
nt	small, between lacrymal and nasal	small, between frontal, nasal lacrymal and maxilla	large, all in maxilla
d	separate	fused	probably separate

Oxydactylus. Since the hypertraguloids are the only other artiodactyls known from this deposit, it seems reasonable to refer the remaining cuboids to this superfamily. Since there are no fused cuboids and naviculars in the size range referable to the Hypertraguloidea, it is reasonable to assume that the bones were separate in all of the species represented in the collections so far.

Affinities. While the teeth agree rather well with the Protoceratidae, the unreduced nasals and the large lacrymal vacuity exclude this genus from close kinship with that family. Certainly the kinship cannot be closer than common ancestry. The facial portion of the skull could be derived from *Leptomeryx*, *Heteromeryx*, or *Leptotragulus*. The posterior position of the internal nares finds its closest parallel in *Leptomeryx*. The derivation of the dentition of this genus from any of the Oligocene Hypertragulidae would involve:

1. Increase in the height of the crown.
2. Loss of the deuterocone on the second and third upper premolars.
3. Increase in the height of the anterior and posterior cusps on both upper and lower, second and third premolars.
4. Development of a postero-internal fold on the second and third lower premolars.
5. Loss of the inner lobe of the heel of the third lower molar.

An examination of the above table makes it obvious that *Nothokemas* cannot claim any close kinship with the tribe Hypertragulini. Probably the greatest difference is in the character of the upper and lower molars, which are more advanced than any other hypertragulid, except *Hypisodus*. *Archaeomeryx* and *Leptotragulus* are very early and very generalized forms which could be close to an ancestral position for many members of this family. At best their kinship with this genus cannot be any closer than that. *Heteromeryx* and *Leptomeryx* are later forms but are still very generalized. *Leptomeryx* is the more specialized of the two. Although the lower jaw of *Heteromeryx* is unknown, the characters of the skull and upper teeth do not indicate close kinship with this genus.

The bones of the feet appear to present rather constant characters among the Mammalia, and their major features are, in most cases, diagnostic of the larger groups. However, in the case of the fusion of the cuboid and navicular, there must have been a period of time when this was a variable character. Many of the genera of the Hypertragulidae are sufficiently well known that the fusion or nonfusion of the cuboid and navicular can be regarded as a constant character. On this basis we can exclude all except *Heteromeryx* and the Leptotragulini

from close kinship with this form. The Leptotragulini are not yet well known from complete skeletons and the reference of the tarsal elements to this group is only probable. *Heteromeryx* is known from a single skeleton only, and it is impossible to determine whether or not the separate cuboid and navicular are constant characters.

Summary. While the dentition of *Nothokemas* has many similarities in common with the Protoceratidae, the facial portions of the skulls are mutually exclusive for close kinship. The dental characters which this genus has in common with the Hypertragulidae are the same characters which that family has in common with the Protoceratidae. Since both families have members in which the cuboid and navicular are separate, this character is of little value in determining the systematic position of the genus. Consequently, in view of the seemingly isolated position of *Nothokemas*, it appears desirable to erect a new family, the *Nothokemadidae* (with the characters of the genus), to receive it.

The references to the literature are given by year and index letter used in the published bibliographies of Hay, and Camp et al.

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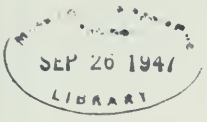
AT HARVARD COLLEGE

Vol. 99, No. 5



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By Benjamin Shreve

CAMBRIDGE, MASS., U. S. A.

PRINTED FOR THE MUSEUM

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No. 5 — *On Venezuelan Reptiles and Amphibians collected by Dr. H. G. Kugler*

By Benjamin Shreve

In the course of his geological work Dr. H. G. Kugler has done considerable zoological collecting in Venezuela and adjacent countries. His earlier collections went to the Museum of Natural History in Basel, Switzerland, where they were reported on, at least in part, by the late Dr. Jean Roux. However, as war conditions prevented Dr. Kugler from sending his 1939–1945 collections to Europe, he generously donated them to the Museum of Comparative Zoölogy with the request that a proportion of the duplicates be sent to Basel. An indication of those sent is given in this report.

Unless otherwise stated, all Kugler localities mentioned are in the Acosta District, Falcón State, Venezuela. Material from Riecito was taken by H. P. Haller who, together with Dr. R. Muhlemann, contributed to the collection. Collecting dates, except for the new forms, are not included, as in general they are too indefinite. The only localities in the first shipment, collected in 1944, were Pauji and Guacharaca, each of which is sometimes followed by the word "area." As the two places are very close together (about 6 miles apart), all this material was catalogued under Pauji. If necessary the Guacharaca specimens can be separated by reference to the field numbers and Dr. Kugler's notes.

Dr. Kugler's notes contain many descriptions of the appearance of the creatures in life. Some of these observations are published below. Included in the collection are a few animals from British Guiana and Trinidad which I have not listed though they are greatly appreciated. In conclusion I should like to say that the Museum of Comparative Zoölogy is extremely grateful to Dr. Kugler and his colleagues for presenting this interesting and valuable collection, mostly from a region in which little collecting has been done.

The following forms are described as new, all type localities being in Falcón State, Venezuela.

Gonatodes caudiscutatus falconensis from Pauji, Acosta District
Tretioscincus bifaseiatus kugleri from Pauji, Acosta District
Leptodeira rhombifera kugleri from Riecito, Acosta District
Oxyrhopus venezuelanus from Pauji, Acosta District

TESTUDINATA

Pseudemys ?scripta subspecies

1 (M. C. Z. 49055) La Penita & Moravita Springs, Cerro Chichiriviche, Silva District.

Possibly this juvenile specimen should be referred to *dorbignyi*, which seems to be a subspecies of *scripta*. Yet it appears unlikely that a Venezuelan turtle is referable to an Argentina form, a point that cannot be decided until a series of Venezuelan adults are available.

SAURIA

Gonatodes caudiscutatus falconensis subsp. nov.

Type. M. C. Z. 48878, a gravid female, from Pauji, Acosta District, Falcón State, Venezuela, collected by H. G. Kugler, June 11 to August 30, 1945.

Paratypes. M. C. Z. 48718, 48879–85 and six Basel Mus. (uncatalogued) specimens. Except that 48718 was collected in 1944, and M. C. Z. 49054 from Ojo de Agua in July, 1945, the rest of the series have the same data as the type.

Diagnosis. Apparently differs from typical *caudiscutatus* only in coloration and possibly larger size. Both sexes of this new form exhibit supraocular spine-like scales, as seems to be the case with *caudiscutatus*.

Coloration in alcohol. Above, brown, sides darker; head indistinctly marked and mottled with grayish and blackish; back with two rows of rather narrow, grayish, transverse bars, each alternating with, or almost meeting its fellow of the opposite series on the vertebral line; tail similarly marked, but the opposing bars usually uniting to form a single, rather irregular series; just preceding each caudal bar, or pair of bars, are two series of blackish spots that meet, or fail to meet, on the mid line, sides and limbs barred or spotted with grayish. Below, gray or grayish brown, throat dotted and marked with light grayish; tail blackish or grayish spotted with white.

Those paratypes, including juveniles, that exhibit the female coloration agree essentially with the type. The backs of some show the kind of black spots described for the tail of the type; darkening of the sides is sometimes scarcely noticeable; ground color of one paratype light grayish brown. Below, similar to type except two which

are very light gray; basal portion of tail often mostly white breaking up into white spots distally, black between the spots.

The six examples showing male coloration differ from the females in the reduction in number, intensity, and often size of the markings which may be more or less obsolete, less reduced on tail; in front of and slightly above the insertion of forelimb is a rather small black-edged ocellus whose white center is often elongate, or ocellus sometimes very indistinct. Below, similar to female, or thighs and hind part of belly lighter. Regenerated tails in both sexes are brown above with obscure, longitudinal, grayish streaks. Below, lighter.

Measurements

	Total length	Head & Body	Tail	Hind limb	Hind foot
Type	90 mm.	45 mm.	45 mm.	19 mm.	8 mm.
Paratypes	49–91 mm.	26–46 mm.	23–48 mm.	11–22 mm.	4–9 mm.

The tip of the tail is regenerated in the type while in many of the paratypes the tail is either regenerated, incomplete, or missing. Extremes of tail measurements are of complete tails.

According to Kugler the coloration of the type in life was: Above, brown-black with a mosaic of dirty olive-green spots; tail with faint pattern of light mauve. Below, throat gray-mauve with dirty yellow spots; belly yellowish gray and olive. He describes a male paratype (Basel Mus.) as having the head and neck olive-green and light brown speckled with yellow; jaws light brown barred with yellow and gray; a white spot rimmed with black on neck; back and flanks dirty olive-brown with seven pairs of dark, angular-shaped spots; tail similarly spotted. An unsexed example is described as having a light brown throat dotted with gray, while that of another unsexed specimen is said to be "light orange."

Gonatodes vittatus (Lichtenstein)

Gymnodactylus vittatus Lichtenstein, 1856, Nomencl. Mus. Zool. Berol., p. 6: La Guaira, Puerto Cabello and Caracas, Venezuela.

1 (M. C. Z. 48719) Pauji
7 (M. C. Z. 48886–90, 48930) El Mene
8 (Basel Mus.) Pauji and El Mene
1 (M. C. Z. 49018) Cerro Cosme
12 (M. C. Z. 49056–60) Rio Ricoa near Cumarebo, Zamora District

M. C. Z. 48930 appears to be in the process of changing from a female type of coloration into that of the adult male. The dorsum is

brownish gray with blackish spots; the vertebral stripe, edged with black on the head, is most sharply defined anteriorly, rather indistinctly so posteriorly. The gular region is strongly marked with black, the belly is white, its sides showing traces of the dark ventral coloring usual in males.

Pseudogonatodes lunulatus (Roux)

Lepidoblepharis lunulatus Roux, 1927, Verh. Nat. Ges. Basel, **38**, p. 252: El Mene, Acosta District, Falcon State, Venezuela.

4 (M. C. Z. 48891–4) Pauji

1 (Basel Mus.) Ojo de Agua

Total length of largest individual 50 (26 + 24) mm.

According to the plate and diagnosis in Parker (1926, Ann. Mag. Nat. Hist. (9), **11**, pp. 293, 297) this gecko is really referable to *Pseudogonatodes*, although left in *Lepidoblepharis* by Burt and Burt (1933, Trans. Acad. Sci. St. Louis, **28**, p. 6).

The head differences cited by Roux (*loc. cit.* p. 254) as a means of separating this form from *P. furvus* Ruthven do not appear to be very constant. More reliable is the fact that in *lunulatus* the scales on the snout are larger and transversely enlarged, especially anteriorly. Apparently *lunulatus* does not grow as large as *furvus*. As stated by Roux the two species differ in coloration. Kugler describes the head and jaws of one as having a "light brown pattern" with a red concavity below the eye.

Thecadactylus rapicauda (Houttuyn)

Gekko rapicauda Houttuyn, 1782, Verhandel. Zeeuwsch. Genoot. Wet. Vlissingen, **9**, p. 323: American Islands.

4 (M. C. Z. 48722, 48900, 49034 & Basel Mus.) Pauji

2 (Basel Mus.) Riecito

Sphaerodactylus molei Boettger

Sphaerodactylus molei Boettger, 1894, Journ. Trinidad Field Nat. Club, **2**, p. 80: Caparo, Trinidad.

? *Sphaerodactylus venezuelanus* Roux, 1927, Verh. Nat. Ges. Basel, **38**, p. 254: El Mene, Acosta District, Falcón State, Venezuela.

10 (M. C. Z. 48720–1, 48895–9, Basel Mus.) Pauji

All ten specimens show much variation in coloration, ranging from a very decorative black and white pattern of longitudinal streaks to

one almost devoid of markings. Some of the latter display a grayish dorsolateral streak. These examples appear to represent *venezuelanus* Roux, but on comparing them with the description and Trinidad specimens of *molei*, no difference in scalation, and no consistent differences in coloration, were found.

The description of *venezuelanus* states that the species has smooth dorsal scales. Under low magnification this appears to be the case, but with high power keels are to be seen.

Possibly this variability is explainable on the grounds that these geckos come from an area of intergradation or hybridization of two different forms. If so, one would appear to be *molei*, while the striped form, of which no pure population appears to be known at present, would be referable to *venezuelanus*. If such a pure population is discovered, it might be predicted that it will be found in the Santa Marta region of Colombia. Assuming all this to be true, *venezuelanus* should then become a race of *molei*, or both races of some other form, possibly of *lineolatus*.

In life the tail of one gecko was "yellow brownish," of another "gray orange and yellow with 6 bars." The throat of the latter was "gray with small dark spots," while two others are described as having "light yellow throats."

Anolis fuscoauratus kugleri Roux

Anolis kugleri Roux, 1929, Verh. Nat. Ges. Basel, **40**, p. 29: El Mene, Acosta District, Falcon State, Venezuela.

3 (M. C. Z. 48727–8, Basel Mus.) Pauji

Total length of largest ♂, 119 (40 + 79) mm., head and body length of gravid ♀, 38 mm., tail incomplete.

In this series the supraorbital semicircles are separated by a single row of scales, while in six specimens of *fuscoauratus* in the Museum collection separation is by two rows; in a seventh anole the number is uncertain. The original description of the type of *kugleri*, however, calls for two to three rows so that more material may show *kugleri* is not a recognizable race, though apparently it does not grow as large as *fuscoauratus*.

The type locality of *fuscoauratus* Duméril & Bibron (1837, Erp. Gén. **4**, p. 110) was said to be Chile, but this is very doubtful for D'Orbigny and Bibron (1847, Voy. Amer. Merid. Rept., **5**, p. 7) give it as Rio Mamoré, between Loreto and the confluence of Rio Sara, Moxos Province, Bolivia. As D'Orbigny was the collector the last

locality is probably correct, and there is apparently no doubt that the two sets of authors were using the same material. This reference has been consistently overlooked in the past, though the accompanying plate (loc. cit., **9**, pl. iii, figs. 1–4), together with the name attributed to D'Orbigny, was cited in Duméril & Bibron's synonymy of *fuscoauratus*, despite the fact that the report on D'Orbigny's reptiles was not published until ten years after the appearance of the Erpétologie Générale, assuming the title pages are reliable. Probably the reference was to a manuscript.

Anolis nitens (Wagler)

Draconura nitens Wagler, 1830, Nat. Syst. Amphib., p. 149: America.
Anolis chrysolepis Duméril & Bibron, 1837, Erp. Gén., **4**, p. 94: ". . se trouve à la Guyane et à Surinam" i.e. Guianas.
7 (M. C. Z. 48723–6, 49035–7) Pauji
1 (M. C. Z. 49050) Riecito

What has been regarded as *chrysolepis* appears to differ from *nitens* only in coloration. Judging by Beebe's (1944, Zoologica (N.Y.), **29**, pp. 197, 200) account, the two apparently occur together in the same sort of habitat, so seem to represent two color phases of the same species. On the basis of the material listed above, together with another Venezuela series in the Museum of Comparative Zoölogy, it appears that those with the *chrysolepis* type of coloration (one example in each series) attain to slightly larger dimensions than the *nitens*, but Beebe's (*loc. cit.* pp. 197–8, 200) measurements of the total length of adults show complete inclusion of *nitens* in *chrysolepis* (165–209 mm., and 136–210 mm. respectively), though his lower figure for *chrysolepis* appears abnormally small.

Dr. Kugler's notes reveal that M. C. Z. 49035–6 were taken in copulation, the female having the light vertebral streak of *chrysolepis*, the male presenting the *nitens* pattern of chevrons, their apices directed posteriorly. This confirms the conspecificity of the two forms. The female held a pair of developing eggs. As the original description of *nitens* is not very diagnostic, there appears to be some doubt about the applicability of the name. If it cannot be used, then *chrysolepis*, which was much better diagnosed, can be employed.

Norops aurata (Daudin)

Anolis auratus Daudin, 1802, Hist. Nat. Rept., **4**, p. 89: Type locality unknown.
1 (M. C. Z. 49052) El Mene

Polychrus marmoratus (Linné)

Lacerta marmorata Linné, 1758, Syst. Nat., ed. 10, p. 208: America.
2 (M. C. Z. 48729–30) Pauji
1 (M. C. Z. 49053) Ojo de Agua

I follow Parker (1935, Proc. Zool. Soc. London, p. 515) in regarding *marmoratus* as a full species, although he admits that the relationship with *liogaster* may be subspecific. Burt and Burt (1933, Trans. Acad. Sci. St. Louis, **28**, p. 40) hold different views.

Of one example Kugler writes: "called Cameleon by local people; changes color according to its surroundings," of another, "beautiful emerald green with brown markings." This specimen shows little trace of green now, being essentially brown with darker markings.

Tupinambis nigropunctatus Spix

Tupinambis nigropunctatus Spix, 1825, Spec. Nov. Lacert. Brasil., p. 18: Brazil.
1 (M. C. Z. 48747) Pauji

Ameiva ameiva ameiva >< praesignis

Lacerta ameiva Linné, 1758, Syst. Nat., ed. 10, p. 202: America.
Cnemidophorus praesignis Baird & Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, p. 129: Panama.
5 (M. C. Z. 48731–5) Pauji

Two of the three larger ones approach *praesignis*, while the third seems nearer *ameiva*. The two juveniles, though closer to *ameiva*, may be too young to exhibit subspecific characteristics.

Cnemidophorus lemniscatus lemniscatus (Linné)

Lacerta lemniscata Linné, 1758, Syst. Nat., ed. 10, p. 209: Guinea, *lapsus calami* for Guiana.
2 (M. C. Z. 48737–8) Pauji
2 (M. C. Z. 49051) Riecito

Regarding one of these lizards, Kugler writes: "Blue-greenish in color; common along roads and in villages, but rarely observed in forests."

Ptychoglossus kugleri Roux

Ptychoglossus kugleri Roux, 1927, Verh. Nat. Ges. Basel, **38**, p. 256: El Mene, Acosta District, Falcón State, Venezuela.
17 (M. C. Z. 48739–42, 48910–6, Basel Mus.) Pauji

Midbody scale rows 29–31 (one not counted); scale rows from second row behind parietals to rear of hind limb 29–30; transverse rows of ventrals from collar to preanals 16–18; supraoculars 3.

Dr. Kugler states that this species is "Never found in bright daylight — it loves dusk or hunts perhaps at night. Above, glossy dark brown; belly salmon colored." Of another he says: "*Ptychoglossus* 165 mm. long. Above, glossy dark brown; belly bright salmon-tomato color." Of a third, "belly light orange and gray." This red or orange color still persists, though considerable fading has taken place since the specimens were received.

Anadia steyeri Nieden

Anadia steyeri Nieden, 1914, Sitzb. Ges. Nat. Freunde Berlin, p. 365: Puerto Cabello, Venezuela.

1 (M. C. Z. 48901) Pauji

Midbody scale rows 44; scale rows from occiput to rear of hind limb 62; scale rows from chin shields to edge of collar 20; femoral pores 7; total length 118 (56 + 62) mm.

The series of femoral pores is interrupted, as mentioned by Roux (1927, Verh. Nat. Ges. Basel, **38**, p. 259), two being at the beginning of the thigh near the preanal region and the remaining five near the knee. Some such arrangement may have occurred in the type in which event Nieden may have included in his pore count the scales separating the two groups of pores.

In coloration our specimen differs from both the type and the example seen by Roux (*loc. cit.*). On either side of the head are two brown, longitudinal lines, the upper extending on to the neck and breaking up into a few scattered spots on the flanks. The longitudinal series of dorsal spots mentioned by Nieden and Roux appear to have fused to form a brown vertebral band about 12 scales in width at midbody.

Bachia lineata Boulenger

Bachia lineata Boulenger, 1903, Ann. Mag. Nat. Hist. (7), **12**, p. 432: Duaca, Venezuela.

45 (M. C. Z. 48736, 48902–9, Basel Mus.) Pauji

Midbody scale rows 24–26; scale rows from occiput to rear of hind limb 42–45. The scale counts of M. C. Z. 48902 are not included, as it is an embryo removed from an egg, and consequently referred to *lineata* with some doubt.

The original description states that the dorsal scales of this species are quadrangular, thus putting it into the *cophias* group of the genus. This may have misled Roux into believing his specimens represented a new form which he (1929, Verh. Nat. Ges. Basel, **40**, p. 31) described as *anomala*, having hexagonal imbricate dorsals as in the *dorbignyi* group. Using other characters besides the shape of the dorsals, Roux, following Ruthven, decided his *anomala* was nearer the *cophias* group.

Burt and Burt (1931, Bull. Amer. Mus. Nat. Hist., **61**, pp. 315–316) in their key to the genus place *lineata* in the *cophias* group, evidently on the basis of Boulenger's statement regarding the shape of its dorsals. *B. anomala* was not included or mentioned, so apparently the Burts had no specimens of it, but the same authors (1933, Trans. Acad. Sci. St. Louis, **28**, p. 57) relegate it to the synonymy of *lineata*, apparently being the first to do so.

Boulenger, when describing *lineata*, stated that it had 5, dark, longitudinal lines on the dorsum. Apparently this is a mistake for no member of the genus I have examined has more than three. Alternatively *anomala* may prove to be distinct.

Tretioscincus bifasciatus kugleri subsp. nov.

Type. M. C. Z. 49039, an adult male, from Pauji, Acosta District, Falcón State, Venezuela, collected by H. G. Kugler between June 11 and August 30, 1945.

Paratypes. M. C. Z. 49038 and 48917 with the same data as the type; M. C. Z. 48743–6 with the same data but collected in 1944; Chicago Natural History Museum 17800 from Cumaná, Venezuela, collected by E. R. Blake, February 13, 1932.

Diagnosis. Similar to typical *bifasciatus* except that the black streak bordering the inside of the light dorsolateral line is more fully developed on each side on both head and body. On the body of *kugleri* only the inner halves of the two median scale rows remain brown, while in every Colombian specimen (presumably representing typical *bifasciatus*) seen, the *whole* of the two central rows, and in some cases all the rows between the light streaks (where the black inner streaks are obsolete) are brown. In the new form there are 16 midbody scale rows; from parietals to rear of hind limb the dorsals number 29–31 (30 in type); femoral pores 5–6 (6 in type) or absent.

Measurements

	Total length	Head & Body	Tail	Hind limb	Hind foot
Type	137 mm.	58 mm.	79 mm.	21 mm.	12 mm.
Paratype 48745	116 mm.	42 mm.	74 mm.	18 mm.	10 mm.
Paratype C.N.H.M. 17800	73 mm.	28 mm.	45 mm.	12 mm.	6 mm.
The remaining paratypes	—	53–58 mm.	—	23 mm.	10–12 mm.

The tail of the type is partially regenerated. That of the paratypes, where no measurement is supplied, regenerated or lost.

Amphisbaena fuliginosa Linné

Amphisbaena fuliginosa Linné, 1758, Syst. Nat., ed. 10, p. 229: America.

1 (M. C. Z. 49049) Riecito

Midbody segment rows 47; body annuli 204; caudal annuli 27.

Mabuya mabouya mabouya (Lacépede)

Lacertus Mabouya Lacépede, 1788, Hist. Nat. Quad. Ovip., **1**, p. 378, pl. xxiv, chart (*partim*): Antilles and Sardinia (restricted by Dunn, 1936 (1935), to the Lesser Antilles).

6 (M. C. Z. 48748–51, Basel Mus.) Pauji

Native name *luzcia* (*fide* Dr. H. G. Kugler).

SERPENTES

Typhlops lehneri Roux

Typhlops lehneri Roux, 1926, Revue Suisse Zool., **33**, p. 298: Pozon, Acosta District, Falcón State, Venezuela.

19 (M. C. Z. 48919–29; Basel Mus.) Pauji

Midbody scale rows 20; dorsal scales from rostral to tail spine about 289–332 (in so small a species it is difficult to make these counts with precision); diameter included in length 31–58 times; total length of largest individual 185 mm., largest gravid ♀ 170 mm. Five of the series contain one or two eggs, a single egg removed from M. C. Z. 48922, measures 26 x 4 mm.

The specimen regarded as an adult *lehneri* by Roux (1927, Verh. Nat. Ges. Basel, **38**, p. 259) appears to be a *Typhlops reticulata* despite Roux's comparison with that form.

Typhlops reticulata (Linné)

Anguis reticulata Linné, 1758, Syst. Nat. ed. 10, p. 228: America.

2 (M. C. Z. 49020–1) Pauji

Midbody scale rows 20; dorsal scales from rostral to tail spine 240–247; diameter included in length 22–24 times.

Leptotyphlops macrolepis (Peters)

Stenostoma macrolepis Peters, 1857, Monatsb. Akad. Wiss. Berlin, p. 402: Caracas and Puerto Cabello, Venezuela.

3 (M. C. Z. 48752–3, 48918) Pauji

Midbody scale rows 14; dorsal scales from rostral to tail spine 229–231; subcaudals 18–19; diameter included in length 39–47 times; length of tail included in total length 14–16 times; total length of largest individual, a gravid ♀ which appears to contain 3 eggs, 315 (295 + 20) mm.

Ninia atrata (Hallowell)

Coluber atratus Hallowell, 1845, Proc. Acad. Nat. Sci. Philadelphia, p. 245: ". . . Colombia, within 200 miles of Caraccas," i.e. Caracas, Venezuela.

4 ♂♂, 3 ♀♀ (M. C. Z. 49025–8, Basel Mus.) Pauji

Midbody scale rows 19; ventrals 139–142 (♂♂), 141–142 (♀♀); subcaudals 55–58 (♂♂), 47–49 (♀♀).

Dryadophis boddaerti ruthveni (Stuart)

Eudryas ruthveni Stuart, 1933, Occ. Pap. Mus. Zool. Univ. Mich., No. 254, p. 4: slopes of San Lorenzo ca. 5,500 feet, Sierra Nevada de Santa Marta, Colombia.

imm. (M. C. Z. 48754) Pauji

Midbody scale rows 17; ventrals 182; subcaudals 118. Both counts are within the range of *ruthveni*, whose juvenile coloration is insufficiently known to assist in determining subspecificity.

Dryadophis boddaerti boddaerti (Sentzen)

Coluber Boddaerti Sentzen, 1796, in Meyer, Zool. Arch., **2**, p. 59: Type locality unknown.

♂, imm. ♂ (M. C. Z. 49022–3) Pauji

Midbody scale rows 17; ventrals 188–194; subcaudals 106+–113. As apparently only 3–4 subcaudals are missing from the truncated tail, the count appears to fall within the range of this subspecies.

The coloration of the adult agrees with that of typical *boddaerti*. The smaller example retains the juvenile pattern, which is not known sufficiently to be diagnostic; its subcaudals are the maximum number for *boddaerti* and just under the minimum for *ruthveni*. Pauji is in a region where intermediates between the two forms are likely to be found.

Spilotes pullatus pullatus (Linné)

Coluber pullatus Linné, 1758, Syst. Nat., ed. 10, p. 225: Asia, in error.

♀ (M. C. Z. 49042) Riecito
head (Basel Museum) Ojo de Agua

Midbody scale rows 18; ventrals 226; subcaudals 113.

Chironius carinatus (Linné)

Coluber carinatus Linné, 1758, Syst. Nat., ed. 10, p. 223: Indies.

head (Basel Museum) Pauji

Scale rows on neck 12. Both *carinatus* and *fuscus* appear to be composite species so that revisionary studies are likely to increase the number of recognizable forms. According to Dr. Kugler's field notes this specimen was jade green above with darkish spots, yellow green on the belly, and 2 meters in length.

Leptophis occidentalis occidentalis (Günther)

Ahaetulla occidentalis Günther, 1859, Proc. Zool. Soc. London, p. 412: Guayaquil and western Ecuador.

♀ (M. C. Z. 48757) Pauji
imm. (M. C. Z. 49041) Riecito

Midbody scale rows 15; ventrals 174 (♀), 168 (imm.); subcaudals 161 (♀), 162 (imm.). The identification, as well as this combination of names, is subject to revision by Dr. J. A. Oliver, to whom the specimens have been sent in connection with his forthcoming monograph of the genus.

Leimadophis melanotus (Shaw)

Coluber melanotus Shaw, 1802, Gen. Zool., **3**, p. 534: Cape of Good Hope, Africa, (after Seba) in error.

♂, ♀, imm. ♂ (M. C. Z. 48755–6, 49024) Pauji
imm. ♂ (M. C. Z. 49040) Riecito

Midbody scale rows 17; ventrals 153–154 (♂♂), 150 (♀); subcaudals 67–71 (♂♂), 68 (♀).

Dipsas nebulata (Linné)

Coluber nebulatus Linné, 1758, Syst. Nat., ed. 10, p. 222: America.
2 ♂♂, ♀ (M. C. Z. 48758, 49029–30) Pauji
♀ (M. C. Z. Basel Mus.) Riecito

Midbody scale rows 15; ventrals 172–181 (♂♂), 169–172 (♀♀); subcaudals 100–102 (♂♂), 85+–90 (♀♀).

Imantodes cenchoa (Linné)

Coluber cenchoa Linné, 1758, Syst. Nat., ed. 10, p. 226: America.
♂ (M. C. Z. 49043) Riecito

Midbody scale rows 17; ventrals 254; subcaudals 159.

Leptodeira rhombifera kugleri subsp. nov.

Type. M. C. Z. 49044, a female, from Riecito, Acosta District, Falcón State, Venezuela, collected by H. P. Haller in 1939.

Paratypes. M. C. Z. 49045–6 with same data as the type; Basel Museum (uncatalogued) from Pauji, Acosta District, collected by H. G. Kugler, June 11 to August 30, 1945; M. C. Z. 38531 from Orinoco River below Ciudad Bolivar, Venezuela, collected by N. A. Weber, January 23, 1935; M. C. Z. 43889 from Guiria, Paria Peninsula, Venezuela, collected by H. A. Beatty, 1937; M. C. Z. 6150 from Trinidad, collected by C. S. Cazabon, no date given.

Diagnosis. Essentially similar to *Leptodeira larcorum* Schmidt and Walker, which I regard as a race of *rhombifera,* but differs in coloration and in often having only 19 midbody scale rows. Instead of a nuchal stripe or "butterfly-shaped marking" on the nape there is, beginning in the post-parietal region, an elongate spot which is more or less completely (in type and some paratypes), or completely divided longitudinally. Where the separation is incomplete the connection may be anteriorly (as in the type), or posteriorly. In this race the dorsal spots appear less likely to coalesce to form an undulating band than in *larcorum.*

Midbody scale rows 19–21 (21 in M. C. Z. 38531 and 43889); ventrals 178–183 (two ♂♂), 177–183 (♀♀); subcaudals 92 (♂♂), 73–87 (♀♀). On one ♀ (M. C. Z. 38531) no ventral count could be made. In the type the midbody scale rows are 19; ventrals 183; subcaudals 83.

	Measurements		
	Total length	Head & Body	Tail
Type	728 mm.	544 mm.	184 mm.
Paratypes	466–719 mm.	350–531 mm.	116–190 mm.

The paratype with the longest (190 mm.) tail has a head and body length of 529 mm., while the one with greatest (531 mm.) head and body length has a tail length of only 142 mm.

Remarks. Not included as paratypes are four examples from Rio Frio in the Santa Marta region of Colombia as they are not typical, seemingly showing evidence of intergradation with some other race. A Bonda snake which appears typical is not included on account of the occurrence in the same region of the four previously mentioned specimens.

Oxyrhopus venezuelanus spec. nov.

Type. M. C. Z. 49031, a male, from Pauji, Acosta District, Falcón State, Venezuela, collected by H. G. Kugler between June 11 and August 30, 1945.

Diagnosis. Apparently most closely related to *Oxyrhopus doliatus* Duméril & Bibron, from which it differs in having a lower ventral and a higher subcaudal scale count, as well as in coloration. Possibly more material may demonstrate that the differences in scutellation are only average.

Description. Eye rather small, its diameter about equal to half the length of the snout which is rounded and feebly projecting; rostral broader than deep, just visible from above; internasals much shorter than the prefrontals; frontal slightly broader than long, as long as its distance from the end of the snout, shorter than the parietals; loreal much longer than deep; preocular 1, reaching the upper surface of the head but separated from the frontal; postoculars 2; temporals 2 + 3; upper labials 8, fourth and fifth entering the orbit; 4 lower labials in contact with the anterior chin shields, which are as long as the posterior; midbody scale rows 19; ventrals 180; anal entire; subcaudals 75, paired.

Coloration in alcohol. Above, head black; a broad, whitish, occipital blotch anterior to the first of 30 black crossbands on the body, 16 on the tail, includes the last half of the parietals; anteriorly the bands extend on to the edges of the ventrals but become progressively complete posteriorly until they form annuli upon the tail; a few bands reduced to about half, developed on one side only, to form a lateral bar or short series of alternating bars; the first six crossbands wider

than the adjacent interspaces, thereafter the bands are usually uniform in width and narrower than the interspaces, which are less uniform; interspaces brownish pink (probably red in life), each scale tipped with black, though the first four or six interspaces show little or no pink (possibly yellow or white in life). Below, yellowish white, uniform except for the encroaching bands and annuli already mentioned.

Measurements

	Total length	Head & Body	Tail
Type	468 mm.	365 mm.	103 mm.

Remarks. The type has been examined by Dr. J. R. Bailey, who is revising the group, and he concurs in considering that it represents an undescribed form.

The La Guaira, Venezuela, snake in the United States National Museum referred to *Clelia doliata* by Stejneger (1901, Proc. U. S. Nat. Mus., **14**, p. 187), as well as two unlocalized specimens assigned to *Oxyrhopus doliatus* var. B. by Boulenger (1896, Cat. Snakes Brit. Mus., **3**, p. 106), also undoubtedly belong to *venezuelanus*.

Pseudoboa neuwiedii neuwiedii (Duméril & Bibron)

Scytale neuwiedii Duméril & Bibron, 1854, Erp. Gén., **7**, p. 1001: Brazil.
♂ (M. C. Z. 49047) Riecito

Midbody scale rows 19; ventrals 191; subcaudals 91; upper labials 8 on right, third, forth, and fifth entering the orbit, 7 on left, third and fourth entering the orbit; loreal absent, a condition that seems quite unusual.

Tantilla melanocephalus (Linné)

Coluber melanocephalus Linné, 1758, Syst. Nat., ed. 10, p. 218: America.
2 ♂♂, 4 ♀♀ (M. C. Z. 48762–5, 49033, Basel Mus.) Pauji
♂ (M. C. Z. Basel Mus.) Riecito

Midbody scale rows 15; ventrals 152–162 (♂♂), 158–164 (♀♀); subcaudals 61–68 (♂♂), 53–57 (♀♀), subcaudal counts of two (♂♀) snakes with truncated tails, not included.

In all these snakes the prefrontal is in contact with the second upper labial, the character used by Schmidt and Walker (1943, Zool. Ser. Field Mus. Nat. Hist., **24**, p. 319) to separate *T. m. capistrata* Cope of arid regions of southern Ecuador and northern Peru from the Amazon race or races. However, they do not state how the race may be separated from other populations of the species. The single specimen

labeled *capistrata* in the Museum of Comparative Zoölogy is from Perico, Peru, and appears to have a much better developed light area in front of the dark nuchal band than is usual. As it is not known to what race these Venezuelan examples belong, I use a binomial.

Stenorhina degenhardtii (Berthold)

Calamaria degenhardtii Berthold, 1846, Abh. Ges. Wiss. Göttingen, 3, p. 8, pl. i, figs. 3–4: Colombia.

2 ♂♂, 2 ♀♀, 3 imm. (M. C. Z. 48759–61, 49032, Basel Mus.) Pauji
imm. (M. C. Z. 49019) Cerro Cosme

Midbody scale rows 17; ventrals 140–153 (♂♂), 149–150 (♀♀), 146–149 (imm.); subcaudals 32–41 (♂♂), 29–30 (♀♀), 29–35 (imm.).

Despite recent recognition of a race from Mexico, only a binomial is used owing to the uncertainty of the subspecific status of Venezuelan examples. Smith and Taylor (1945, U. S. Nat. Mus. Bull. 187, p. 132) revert to the original spelling of *Stenorrhina*. As that spelling appears to be only a *lapsus calami* (c.f. Rules of Zoological Nomenclature, Article 19), the change seems unnecessary.

Trimeresurus ?atrox (Linné)

Coluber atrox Linné, 1758, Syst. Nat., ed. 10, p. 22: Asia, in error, restricted to Surinam by Schmidt & Walker (1943).

imm., 2 heads (M. C. Z. 48766, Basel Mus.) Pauji

Midbody scale rows 25; ventrals 213; subcaudals 72. This immature example is referred to *atrox* with considerable misgiving, as its second upper labial is separated from the pit, in addition to other minor differences.

Regarding the larger fer-de-lance represented only by a head, Dr. Kugler writes: "5 feet, 11 inches, very dark species."

Crotalus durissus terrificus (Laurenti)

Caudisona terrifica Laurenti, 1768, Spec. Synops. Rept., p. 93: America.

head & rattle (M. C. Z. 48767) Pauji
♂ (M. C. Z. 49048) Riecito

Midbody scale rows 31; ventrals 167; subcaudals 31. The scale row formula (27–31–23) is higher, except perhaps anteriorly (where the skin of the neck is so distorted that the count cannot be made with certainty), than that of any of the 76 specimens seen by Gloyd (1940, Chicago Acad. Sci., Spec. Publ. No. 4, p. 133). The body is skinned out with head and tail attached.

AMPHIBIA

Caecilia subnigricans Dunn

Caecilia subnigricans Dunn, 1942, Bull. Mus. Comp. Zoöl., **91**, p. 511: Magdalena River, Colombia.

1 (M. C. Z. 26141) Riecito

Primary annuli 158, secondaries 27; diameter included in length 32 times; total length 161 mm.

Both primary and secondary counts are hard to make accurately; my figures for both differ from those of Dr. E. R. Dunn, who kindly examined the specimen. Before submitting it to Dunn I had referred it provisionally to *subnigricans*, a disposition with which he agreed. Dr. Dunn invited my attention to a patch of teeth at the tip of the lower jaw, a condition sometimes found in other immature caecilians, but apparently not in adults.

Bufo typhonius sternosignatus Günther

Bufo sternosignatus Günther, 1858, Cat. Batr. Sal. Brit. Mus., p. 68, pl. v, fig. C: Mexico and Cordova, Mexico, also Venezuela and Puerto Cabello, Venezuela. Restricted to Venezuela by Boulenger (1882).

3 (M. C. Z. 25976–7, 26152) Pauji

1 (M. C. Z. 26151) Cerro Cosme

Even though *Bufo typhonius alatus* Thominot (1884) from Panama should prove to be synonymous, *sternosignatus*, being the older name, will have to be used.

Leptodactylus bolivianus Boulenger

Leptodactylus bolivianus Boulenger, 1898, Ann. Mus. Civ. Stor. Nat. Genova (2), **19**, p. 131: Barraca and Missiones Mosetenes, Bolivia.

4 (M. C. Z. 25985–8) Pauji

1 (M. C. Z. 26143) Riecito

A male in this series has two black asperities on each thumb, instead of the one called for by the original description.

Leptodactylus diptychus Boulenger

Leptodactylus diptychus Boulenger, 1918, Ann. Mag. Nat. Hist. (9), **2**, p. 431: Andes of Venezuela.

2 (M. C. Z. 25989–90) Pauji

Leptodactylus caliginosus Girard

Leptodactylus caliginosus Girard, 1853, Proc. Acad. Nat. Sci. Philadelphia, p. 422: Rio de Janeiro, Brazil.

6 (M. C. Z. 26144–6) Cerro Cosme

Whether frogs from northern South America, usually referred to *caliginosus*, are really the same as those from Rio de Janeiro, seems questionable.

Hyla crepitans Wied

Hyla crepitans Wied, 1825, Beitr. Naturg. Brasil., **1**, p. 525: Tamburil region, interior of Bahia State, Brazil.

6 (M. C. Z. 25978–83) Pauji

1 (M. C. Z. 26142) Riecito

Dr. H. G. Kugler contributes several notes, about these frogs which may be summarized as follows: Above, white, almost silver white, with large black eyes whose grayish yellow lids have "a fine black ring around the base" (no trace of this is to be seen in the preserved specimen referred to); finger tips and belly light yellow. One pair, taken in embrace, had brownish markings on a yellowish ground; another mating pair, removed from a test pit, exhibited brown marblings exactly the shade of the soil. The brown markings of others closely resembled the tree-bark on which the frogs were resting, for they change color readily.

They remain quiet except shortly before dawn and dusk when they emit calls, and during the mating season, when they croak at night. Some eggs, placed in a washbasin by Kugler, hatched within forty-eight hours. The species has a pleasant fruity smell and is locally called Rana Capina.

Hyla misera Werner

Hyla misera Werner, 1903, Zool. Anz., **25**, p. 252: Caracas, Venezuela.

1 (M. C. Z. 26150) Cerro Cosme

An adult ♂, head and body length 21 mm. Outer and middle fingers about a third webbed instead of half as called for in the original description. On the back is an elongate X-shaped figure not mentioned in the description; nevertheless the identification seems to be correct.

Hyla boulengeri (Cope)

Scytopis boulengeri Cope, 1887, U. S. Nat. Mus. Bull. 32, p. 12: Nicaragua.
1 (M. C. Z. 25984) Pauji

Mr. R. D. Hamilton of the University of Michigan believes that Venezuelan frogs included under this name represent more than one form. Pending the results of his investigation, I refer this frog to *boulengeri* while observing that the few Venezuelan examples I have seen differ in coloration from topotypical *boulengeri.*

Phyllobates trinitatis Garman

Phyllobates trinitatis Garman, 1887, Bull. Essex Inst., **19**, p. 13: Trinidad.
7 (M. C. Z. 26147–9) Cerro Cosme

Head and body length of largest frog, 27 mm.

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